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## DEFINITION OF AN ESTUARY.

An estuary is the region at the mouth of a river where the salt water of the ocean meets the fresh river water, and by the force of the rising tide reverses the current of the river, causing the fresh water to flow back over its shores.

In the Spey, which is the swiftest river in Britain, salt sea-water is forced, like a dense fluid wedge, for a considerable distance up the bed of the river by the rising tide, and lifts the fresh stream to a higher level, so that perfectly fresh water is found on the surface, separated by a brackish layer a foot or two thick from the salt water below. The salt wedge is withdrawn by the ebb tide, and the river current resumes its rapid flow to the sea. . . . .

In such an inlet as that of the Thames or the Firth of Tay, where the river is large, the water is found to grow rapidly salter from river to sea, the surface is much fresher than the lower layers, and the change of salinity between high and low tide is very marked. This form of river entrance is appropriately called an *Estuary*. When, however, the inlet is very large compared with the river, and when there is no bar at the opening, the estuarine character is only shown at the upper end. In the Firth of Forth, for example, the landward half is an estuary, but in the seaward half the water has become more thoroughly mixed, the salinity is almost uniform from surface to bottom, and increases gradually toward the sea. (Mill, 1892, paragraphs 230, 231.)

The rising tide of the ocean apparently has two effects: first, the advancing wall of salt water acts as a barrier against the river current, and is strong enough to reverse the direction of its flow; and second, a stream of salt water is forced up the bed of the river, lifting the fresh. In other words, the influence of the tide extends up the river for a greater distance than does the salt water, and the term *estuary* is applied to the region where the shores are at each high tide inundated by fresh water.

On the Hudson River there is a tidal range of three feet at Troy, New York (U. S. Coast and Geodetic Survey, 1923, p. 352), more than 150 miles from the mouth of the river, and the extent of tidal shore where the water is not at all saline probably exceeds 50 miles. On the Kennebec River, in southern Maine, plants characteristic of salt marshes are found for only a short distance above Bath, near the mouth, while the tide rises and falls more than four feet at Augusta (U. S. Coast and Geodetic Survey, 1923, p. 347), 30 miles up the river (see Pl. 6). At Richmond, midway between Augusta and Bath, the chlorine in the water reaches 870 parts per million on the flood tide, and is greater on the bottom than at the surface (Whipple, 1907, p. 187), but is not sufficient to prevent the river water from being used for the town's water supply. On the St. Lawrence River, the estuary is the tidal part of the river from St. Jean-Port-Joli, 50 miles below the city of Quebec, to the head of tide, near Three Rivers. At St. Jean-Port-Joli the water becomes saline, and the shores support salt-marsh plants (Svenson, 1927, p. 89).

## PREVIOUS WORKERS ON ESTUARIES.

These estuarine conditions undoubtedly obtain on all rivers except those which enter the ocean by falls, but this paper treats only those of the coast from Chesapeake Bay to the St. Lawrence River, since these estuaries, by reason of their similar geological histories and distinctive flora, seem to constitute a group. The rivers entering Hudson Bay may also belong with this group, but they have been very little botanized. Indeed, in our own region, estuaries are among the least-known localities.

The first estuary to which the attention of botanists was called was that of the Delaware River. Since the shores of that river are estuarine about Philadelphia, it was natural that botanists should have discovered early that unusual plants were to be found there. Pursh apparently collected on the tidal flats, for he described (1814, p. 238) *Peplis americana* (*Elatine americana*) as being "inundated during its flowering time, in slow-flowing places of rivers, in Pensylvania," and this species is almost entirely confined to estuaries, including that of the Delaware.



In 1817 several discoveries were made in the vicinity of Philadelphia. Thomas Nuttall (1817), in company with Professor B. S. Barton, discovered on the tidal flats of the river *Tillaea simplex* (*T. aquatica*), "*Limosella aquatica*, var. *tenuifolia*," *Crypta minima* (*Elatine minima*), and *Hemianthus micranthemoides* (*Micranthemum micranthemoides*). In the previous year, *Limosella* had been discovered by H. N. Fenn and M. C. Leavenworth at New Haven, Conn., while Dr. Eli Ives had found it on the estuaries of the Housatonic and other rivers of southern Connecticut. The latter collector distinguished the plant from *L. aquatica*, var. *tenuifolia*, and described it as *L. subulata* (Ives, 1817, p. 441). In 1829 William Oakes found this species on Nantucket Island, and ten years later he and Tuckerman collected it at Plymouth, Mass. Since then its known range has been gradually increased until now we have collections of this *Limosella*, usually on estuaries, sometimes on brackish sandy shores, from Delaware northward into Newfoundland, and along the shores of the Gulf of St. Lawrence.

Nuttall (1841, p. 361) described from the vicinity of Philadelphia *Diodonta bidentoides* (now *Bidens bidentoides*), which became famous as one of the specialties of this region. Following its discovery there were many collections of this plant by Elias Durand, William Canby, A. H. Smith, and C. F. Parker, while we find a short discussion of this and of other species of the same habitat by T. C. Porter (1872). *Bidens bidentoides* has since been found on several estuaries, from Chesapeake Bay to the Hudson River.

Several of the rivers entering Chesapeake Bay have been found to have endemic plants at their mouths. In 1903 Professor G. H. Shull published a discussion of *Isoëtes saccharata*, a species confined to this region, on shores overflowed by fresh water at high tide.

In 1902 Mr. A. A. Eaton discovered a strange *Bidens* on the estuary of the Merrimac River, which Professor M. L. Fernald pronounced a relative of *B. bidentoides*. This species, *B. Eatoni*, has since been found from the Hudson River to southern Maine, always confined to estuaries. The genus *Bidens*, owing principally to the work of Professor Fernald, has been found to contain three exclusively estuarine species, which usually appear in a slightly different form on each river where they occur.

Largely through the work of Professor Fernald and Mr. Bayard Long, it has become evident that there are many species on the northeastern Atlantic coast of North America which are confined to estuaries, and others which have estuarine stations lying far from their general ranges. It has been shown that estuarine plants are to be sought not only from southern New England to Chesapeake Bay, but on the river mouths of Maine, New Brunswick, and southern Quebec.

It was in an attempt to botanize systematically the estuaries along this coast that in August, 1923, Mr. H. K. Svenson and I collected on the river mouths from that of the St. Lawrence to Northumberland Strait, and on the coast of Maine. This work was continued in August, 1924, when, in company with Mr. R. W. Storer (Harvard '25), I botanized the shores of the St. John River (previously visited by Professor Fernald) and along the northern coast of Nova Scotia. I have also had opportunity to visit many estuaries in Connecticut, Massachusetts, and New Hampshire, and have in all botanized some seventy estuaries, from that of the Hudson to that of the St. Lawrence.

## TEMPERATURE AND SALINITY ON ESTUARIES.

The plants which grow on the shores of these estuaries are living under most unusual conditions, for they are submerged twice a day by fresh, or slightly brackish, water. Moreover, the water sometimes carries in suspension a large amount of silt, which, as the tide ebbs, is deposited upon the plants, and at low tide is baked into a hard crust. The mud along the shores is often several decimeters deep, and the rocky places are covered with a slimy mud coating (see Pls. 14, 15).

At low tide the sun warms the mud, and the water as it flows back over the flats becomes several degrees warmer than the open water of the ocean, or that of the river above its tidal shores. At Woolwich, Maine, on the lower part of the Kennebec River estuary, the temperature of the water on September 8, 1924 (a day when the sun was not very bright) was 21° Centigrade; the salt water of that part of the Gulf of Maine seldom exceeds 18° C., even in July and August. Table 1 shows comparative temperatures for a few dates in July and August, 1925. The figures in the column headed "Monmouth" were kindly supplied to me by Mr. W. A. Whiting, Superintendent of the State Fish Hatchery in Monmouth, Maine. The Fish Hatchery is on a brook which flows into Cobbosseecontee Stream,



a tributary of the Kennebec River which enters the estuary at Gardiner. These temperatures may therefore be taken as characteristic of the water flowing into the estuary, although they are somewhat lower than many parts of Cobbosseecontee Stream, having been taken in the shaded tanks in which trout and salmon fry are raised. The column headed "Gardiner" represents temperatures taken on the Kennebec

TABLE 1.

*Comparative temperatures of water at three localities in Maine in 1925.*

| Date | Time | Boothbay Harbor | | Gardiner | | | Monmouth |
|---|---|---|---|---|---|---|---|
| | | Air | Water | Air | Water | Weather | Water |
| July 13 | Noon | 26.5 C. / 80 F. | 15.5 C. / 60 F. | 22.0 C. / 72 F. | 24.5 C. / 76 F. | Sunny | 16.5 C. / 62 F. |
| July 14 | Noon | 25.5 C. / 78 F. | 15.5 C. / 60 F. | 25.5 C. / 78 F. | 23.5 C. / 74 F. | Sunny | 16.5 C. / 62 F. |
| July 15 | Noon | 24.5 C. / 76 F. | 16.5 C. / 62 F. | 28.5 C. / 83 F. | 25.0 C. / 77 F. | Sunny | 16.6 C. / 62 F. |
| July 16 | Noon | 22.0 C. / 72 F. | 16.5 C. / 62 F. | 26.0 C. / 79 F. | 22.5 C. / 73 F. | Cloudy & showery | 16.5 C. / 62 F. |
| July 19 | Noon | 26.5 C. / 80 F. | 16.5 C. / 62 F. | 25.0 C. / 77 F. | 24.5 C. / 76 F. | Sunny | 16.5 C. / 62 F. |
| July 29 | 4 p.m. | 26.5 C. / 80 F. | 18.0 C. / 64 F. | 25.0 C. / 77 F. | 22.5 C. / 73 F. | Sunny | |
| July 30 | Noon | 19.0 C. / 66 F. | 16.5 C. / 62 F. | 24.5 C. / 76 F. | 21.0 C. / 70 F. | Sunny | 11.5 C. / 53 F. |
| July 31 | Noon | 21.5 C. / 71 F. | 16.5 C. / 62 F. | 23.5 C. / 74 F. | 21.0 C. / 70 F. | Sunny | 12.0 C. / 54 F. |
| Aug. 1 | Noon | 21.0 C. / 70 F. | 15.5 C. / 60 F. | 20.0 C. / 67 F. | 20.5 C. / 69 F. | Cloudy & showery | 12.0 C. / 54 F. |
| Aug. 3 | Noon | 25.5 C. / 78 F. | 16.5 C. / 62 F. | 28.5 C. / 83 F. | 22.5 C. / 73 F. | Sunny | |
| Aug. 3 | 4 p.m. | 25.5 C. / 78 F. | 16.5 C. / 62 F. | 25.0 C. / 77 F. | 19.0 C. / 66 F. | Sunny | |
| Aug. 5 | Noon | 26.5 C. / 80 F. | 17.5 C. / 64 F. | 27.0 C. / 81 F. | 26.0 C. / 79 F. | Sunny | 14.0 C. / 57 F. |

estuary. Most of the readings in Gardiner were made by Miss Katherine H. Knight, of that city. For the readings taken at Boothbay Harbor, I am indebted to the Superintendent of the U. S. Fish Hatchery there; these may be taken as characteristic of the salt water entering the estuary.

Observations made near Boothbay Harbor show to what extent water may be warmed by flowing over sun-baked shores. Little

River, in the town of Boothbay, is an arm of the sea, two miles long and a quarter of a mile wide, salt for its entire length. Here the rocks are heated at low tide as on an estuary, and here, at the head of the inlet, the temperature of the water was found to be 21.5° C., nearly four degrees warmer than the air, while at the same time the temperature nearer the ocean in this same inlet was 16.5°, and that of a small brook entering the warmest part of Little River was only 12°.

When fresh water pours into salt water, it is evident that they will to some extent mix, and that there will be a transition from one to the other. As the salt water has the greater density, the salinity will be less at the surface than at a depth; this, it has been shown, is the case even in the open water of the Gulf of Maine (Bigelow, 1914, p. 44) and in the Bay of Fundy (Mavor, 1923, Pl. 9). Salinity tests at various depths and conditions of tide on the estuaries of several rivers in Scotland have shown the salt content of the water to be a very variable factor. Table 2 shows in a striking manner the extent to which salt water runs under the fresh layers, and at what depths they mix.

TABLE 2.

*Salinity of the River Spey.**

| Depth in Feet | Half Flood Tide | | Ebb Tide | |
|---|---|---|---|---|
| | Percentage of Fresh Water | Percentage of Salt Water | Percentage of Fresh Water | Percentage of Salt Water |
| 0 | 99 | 1 | 99 | 1 |
| 1 | 92 | 8 | 99 | 1 |
| 2 | 84 | 16 | 99 | 1 |
| 3 | 44 | 56 | 99 | 1 |
| 4 | 36 | 64 | 99 | 1 |
| 5 | 8 | 92 | 99 | 1 |
| 6 | 8 | 92 | 33 | 67 |
| 7 | 8 | 92 | 20 | 80 |

*Mill and Ritchie, 1891, p. 468.

Whipple (1907, p. 187) has made similar tests at Richmond, Maine, on the estuary of the Kennebec River, but here the salt water was present in such small quantities that it did not rise to a level where it would affect the plants on the shores of the river.

By titration of water samples with silver nitrate, using potassium dichromate as an indicator,[1] I have determined the salinity at various points on several estuaries, but have confined my tests to surface water, and to the water left standing on the flats at low tide. I have, therefore, been able to get only the relative salinity of neighboring spots. Thus, of the water left on the flats at low tide, the salinity is greater on the low places than on the high, just as might be expected. The water becomes more saline as one goes down the river towards the ocean, also at each locality as one goes nearer the low-tide level. A plant like *Spartina alterniflora* Loisel. (*S. glabra* Muhl., var. *alterniflora* (Loisel.) Merr.; see Fernald, 1916, p. 177), which usually grows in pure sea water, will be found over the whole shore at a place where the water is saline, but going upstream, toward fresher water, it will be confined near low-tide level, where it is covered more deeply at high tide, hence better supplied with salt water than at the high places. This principle is shown in Plate 14, figure 1, a photograph taken at Woolwich, Maine, on the Kennebec estuary. The water here is rather saline, but there is a cove where a small stream enters, making the water there a little fresher. On the lower levels, where the water is somewhat saline (that left in pools at low tide, after it had been considerably diluted by fresh water, is 12 per cent[2]), *Zizania aquatica* L., which is somewhat tolerant of salt (Scofield, 1905), dominates; in the foreground the salinity is a little less (10 per cent), and here *Lophotocarpus calycinus*, var. *spongiosus*, abounds; while where it is reached only by the surface water at high tide, which is 0.6 per cent saline, a variety of *Bidens Eatoni* occurs.

This locality at Woolwich is shown in a little more detail in Plate 7, figure 1, which pictures the same locality as the photograph. Where reached, at high tide only, by fresh water floating on the surface of the salt, is *Bidens Eatoni*, var. *interstes* (2). A small mound to the right is also high enough to be bathed only at high tide, hence by fresh water; here grow *Sium suave* and *Sparganium eurycarpum* (6). On slightly lower ground, where reached by more brackish water at high tide, is *Lophotocarpus calycinus*, var. *spongiosus* (1). Below

[1] I am indebted to Mr. S. S. Kurtz (Harvard '21) for directions for carrying out these analyses. A brief discussion of this method may be found in Olsen (1919, p. 350).

[2] The salinity is here expressed, not in parts of salt per thousand, but in percentages, sea water from the shore at Ocean Point, Boothbay, Maine, being taken as 100 per cent saline. Thus a mixture of equal parts of sea water and fresh water is 50 per cent saline.

this are *Scirpus nanus* (3) and *Spartina alterniflora* (4), the latter extending well below the limits of this map, to low-tide level. *Zizania aquatica* (stippling) and *Scirpus acutus* (rings) here show considerable tolerance of salinity, mixing with the *Spartina*.

Conditions affecting the salinity are very complex: currents, entrant streams of fresh water, the character of the shore and of the bottom, and doubtless recent rainfall and even the temperature, all have their effects. Above this locality at Woolwich, the river has rocky shores, and the vegetation becomes again that of the salt marsh, except where fresh water enters. Plate 7, figure 2, shows the situation at a place where the shore is a clay bank instead of a rocky cliff, and there are a few springs of fresh water in the flats. *Scirpus americanus* and *S. acutus* Muhl. (see Fernald, 1920), both tolerant of salt water, predominate, but, where the springs occur, *Lophotocarpus* is present. The salinity of the water left on the surface of the mud at low tide was 8.48 per cent in the patch of *Lophotocarpus*, and 13.33 per cent where the *Scirpus* grew.[1] At high tide the surface water above the *Lophotocarpus* had not enough salt to be detected by the titration method, although a slight precipitate could be obtained by pouring a large amount of silver nitrate on the surface of the water. At the same time, surface water over the *Scirpus* showed a salinity of 1.81 per cent. The bottom water would undoubtedly be more saline, but in much the same proportion for the two places. Plate 14, figure 2, is a photograph of this locality.

Another place on the estuary of the Kennebec, where a brook enters the river, may be considered (Pl. 14, fig. 3). Here the flats are covered with *Scirpus acutus* and *Zizania aquatica*, both of which are tolerant of some salinity. The map (Pl. 7, fig. 3) tells the story better than it can be expressed in words. The shore from high to low-tide levels is shown, with one-foot contour lines; the water level is represented as at low tide. The fresh water of the Kennebec River flows as from the upper left of the map, and a brook enters from the upper right. Salt water from the Atlantic Ocean comes as from the lower part of the map. First, *Spartina alterniflora* is dominant, and at higher levels one finds *Lilaeopsis lineata*, which grows in

[1] It must be borne in mind that these figures do not indicate either the maximum or the minimum salinity to which the plants are subjected. They are merely for comparison of the two places. The salinity changes with the tide; at high tide the bottom water may be much more brackish than are the pools left when the tide has receded.



slightly diluted sea water (section A). Then (section B) at the higher levels the water becomes fresh enough to be tolerated by *Lophotocarpus*, while *Spartina* is confined to the lower levels. In section C, *Lophotocarpus* has moved to the lower levels, for as we go upstream the water on the higher levels becomes too fresh for it. At high-tide level a few springs are making the water more fresh, and here *Sagittaria latifolia*, *Alisma Plantago-aquatica*, and *Bidens hyperborea*, var. *colpophila*, find conditions suitable for their growth. In section D, *Lophotocarpus* is confined to the lower levels, while on the higher levels *Pontederia cordata*, *Bidens*, *Sagittaria latifolia*, *S. graminea*, *Tillaea aquatica*, and other fresh-water species become abundant. Finally, at section E and above it, all the water is fresh, and the fresh-water plants extend to the lowest levels, while *Potamogeton epihydrus* grows in the brook below low-tide level.

Here, in Plate 7, figure 3, we may trace the search of each group of plants for the salinity preferred. *Spartina* is found first reaching nearly to high-tide level; a few rods below the lowermost point on the map, it is abundant over the whole shore. Gradually, as it goes up stream, *Spartina* seeks lower and lower levels, following the salt water. *Lophotocarpus*, next, starts near the high-tide mark, and moves toward the low-tide level as it goes up stream. The fresh-water types, which are at first confined to the high-tide level, find the lower altitudes more suitable for them as they go upstream where less salt water penetrates.

Salinity tests at this point gave somewhat surprising results. At high tide, titration of surface water at sections A and B gave no indications of salt content, although silver nitrate poured into the river gave a slight precipitate. At section B a floating pier made it possible to go out 30 feet from the shore; everywhere the *surface* water was almost fresh, and on the logs which floated the pier, where often wet by the waves, grew *Lenzites sepiaria*. This indicates that the salt water must run well under the fresh, but also that *Spartina alterniflora* is somewhat tolerant of a percentage of fresh water.

It must be remembered that the subsaline types are found only at the lower part of the estuary. On the Kennebec the estuary extends 25 miles above the localities just discussed, and is covered with fresh-water types from high-tide to low-tide levels.

Fernald and Long found a few individuals of *Lophotocarpus* on the tidal shores of the Cathance River, a tributary to the Kennebec, where they were reached by practically no salt water, and specimens

of *Bidens* and other fresh-water plants are sometimes found in brackish water, but they are depauperate and obviously out of their proper environment. These exceptions are hardly of sufficient weight to affect the validity of these generalizations concerning the altitudinal distribution of estuarine plants as controlled by salinity.

The Kennebec is only one of the many rivers with estuarine conditions at their mouths, and here this problem of altitudinal distribution of plants has hardly been touched upon. To what extent these facts hold true on other rivers must remain for future investigation; my observations have indicated that conditions are very similar elsewhere. On the rivers entering the Gulf of St. Lawrence from eastern New Brunswick, however, the varieties of *Bidens hyperborea* present in this region seem to be more tolerant of salinity than are those of the Kennebec, and often grow intermixed with *Lophotocarpus*.

## EFFECTS OF ESTUARINE CONDITIONS ON VEGETATION.

Semidiurnal submergence, warm water, copious deposits of mud, and varying salinity make the estuary a specialized and extreme habitat. Many plants of fresh water, such as *Pontederia*, *Alisma*, *Scirpus cyperinus*, var. *pelius*, species of *Potamogeton*, *Utricularia*, and *Sagittaria*, and the like, are abundant on estuarine shores, but there are other plants which react to these conditions so as to become almost unrecognizable. *Sium suave* Walt. (*S. cicutaefolium* Schrank; see Blake, 1915, p. 137), which is normally an erect plant one or two meters high, with pinnate leaves, becomes creeping, often rooting at the nodes, with leaves reduced usually to a single leaflet, having in their axils bulblike structures bearing fascicles of round or ovate leaves less than a centimeter in diameter. This phase of *Sium suave*, which has been described as forma *fasciculatum*, occurs regularly on the estuaries of the Kennebec and the Sheepscot Rivers, and has been found two or three times on the shores of drying ponds late in the season. Its occurrence on these pond shores may be explained as follows: the plant had been growing under water, and had assumed the lax state of forma *Carsonii* (see Fassett, 1921b, p. 113); the level of the water being lowered, the *Sium* was left stranded on the mud, lying flat on the surface of the soil, where, instead of recovering its upright position, it sent up at the nodes little clumps of leaves which reverted to the simple form sometimes found in seedlings of this species. On the two estuaries mentioned above, the action is probably somewhat similar to this, the rush of



water at high tide making an upright position difficult for the plant, and the low tide leaving it prostrate on the mud. This theory is strengthened by the fact that *Sium suave* is sometimes found on the estuary of the Kennebec growing where its stems are supported by a thick tangle of grasses and sedges, or where the action of the water is slight, and in these situations it keeps its typical form. All gradations may be found between the erect plant and forma *fasciculatum*. On most of the other estuaries *Sium* holds its normal form, although on the Penobscot and the Union Rivers in Maine it ordinarily becomes short and stout, apparently better to resist the action of the water. Is this variability in reaction due to differences in the various estuaries, or to different races of the species, which are without morphological characters, but which act differently when subjected to the same treatment?

*Leersia oryzoides*, forma *glabra* (Eaton, 1903), which lacks the usual scabrosity of the species, was described from the estuary of the Merrimac River, and also occurs where inundated at high tide on the Kennebec River. A single shrub of *Myrica Gale*, which was stranded on the tidal flats of the Kennebec estuary, developed under the unusual conditions very short and thick coriaceous leaves.

Perhaps the most profound modification under estuarine conditions is that of *Epilobium glandulosum*, var. *ecomosum* (Fassett, 1924a), which matches specimens of ordinary *E. glandulosum*, var. *adenocaulon* (Fernald, 1925d, p. 35), except for the complete lack of coma on the seeds. Presence of the coma is the distinguishing character of the tribe *Epilobiae* of the *Onagraceae*, but this basic structure seems to have been lost in the adaptation of a normally wind-disseminated plant to estuarine conditions.

There are problems awaiting the physiologist on estuaries. What goes on within the cell of the plant which has adapted itself to conditions of alternate drowning and baking, or to water of varying salinity? How is the pollen protected in a flower which is dry only a few hours each day? The way in which pollination is effected in some estuarine species has recently been studied by Dr. F. W. Pennell (1924).

## DISRUPTED RANGES OF ESTUARINE PLANTS.

Far more important to the plant geographer than the plants undergoing sporadic modifications when growing on tidal shores are those species which are confined to estuaries, or have estuarine stations separated by long distances from the rest of the range. Several examples may be mentioned: *Lophotocarpus calycinus*, var.

*spongiosus* (Pl. 11, fig. 2), an offshoot from the species of the Mississippi Basin, is found on river mouths from Maryland to eastern New Brunswick; *Cardamine Longii* has been found in only three or four patches on the Kennebec estuary; *Scirpus Smithii*, var. *levisetus*, grows on the Kennebec and the St. Lawrence estuaries; *Isoëtes saccharata* (Pl. 11, fig. 4) is confined to the estuaries of rivers flowing into Chesapeake Bay; and *Gentiana Victorinii* is endemic to the estuary of the St. Lawrence River. Spectacular "jumps" are found: we see such ranges as that of *Nymphozanthus advena* (Pl. 10, fig. 4), common eastward to the Hudson River, barely penetrating New England in southwestern Connecticut, then reappearing in great abundance on the tidal flats at the mouth of the Kennebec River, 250 miles away; or of *Scirpus fluviatilis* (Pl. 10, fig. 2), whose eastern limit is the Hudson-Champlain Valley and the Boston region, except for outpost stations on the estuaries of the Merrimac and the Kennebec Rivers, and a single station in New Brunswick on the estuary of the St. John River. Of great importance on these river mouths is the genus *Bidens*, already mentioned in connection with Professor Fernald's work. The remarkable members of this genus will be discussed in detail presently, but they will be better understood if we first consider how such endemic estuarine floras could have arisen, and why we find on estuaries many species characteristic of regions considerably to the southward.

## PLANTS WITH ESTUARINE OUTPOST STATIONS.

There is a group of plants which throughout the greater parts of their ranges are not estuarine, being found on pond shores, river banks, and in various aquatic habitats, but beyond the limits of these continuous ranges they have one or more outpost stations on estuaries. Since the outpost stations are usually to the north of the rest of the range, it seems probable that these plants once enjoyed a general distribution during a warmer epoch, and have since died out in the northern parts of their ranges, except where bathed by the warm water of the estuaries. In this they may be comparable to *Scirpus Hallii* and *Echinodorus tenellus*, which seem to be relics of a former period of more favorable climate that have died out in the latitude of Boston, except in such apparently suitable places as the famous Winter Pond in Winchester, Mass.

**Sagittaria heterophylla** Pursh, including formae *elliptica* (Engelm.) Blake, *rigida* (Pursh) Blake, *fluitans* (Engelm.) Blake, and *gracilis*



(Pursh) Rob. (See Blake, 1913, p. 159). (Pl. 9, fig. 1.) From Minnesota, Nebraska, and Missouri eastward to Quebec, Lake Champlain, and eastern Massachusetts, southward to Virginia, *Sagittaria heterophylla* is characteristic of aquatic habitats, not estuarine. From Montreal it follows down the St. Lawrence River to the estuary, where it is abundant. Its outpost station is on the estuary of the Kennebec River, and is the only locality in Maine where this plant grows, a hundred miles from its nearest station in Massachusetts. In eastern Massachusetts it appears to be confined to that part of the Merrimac Valley which underwent marine submergence in early postglacial times.

**Echinochloa muricata** (Michx.) Fernald (1915). Common from Maine to Florida, westward to Illinois, Kansas, Oklahoma, and New Mexico (Wiegand, 1921, p. 57). This species ranges eastward to the valley of the Penobscot River, in eastern Maine, whence it "jumps" to the estuary of the St. John River, where it has been found at but one station, at Burton, New Brunswick.

**Zizania aquatica** L.; Fassett (1924b, p. 156). (Pl. 9, fig. 2.) This is the larger Wild Rice found in New England, treated by Hitchcock (1908, p. 124) as *Z. palustris*. It ranges along the Atlantic coast in quiet, usually fresh, water, from Florida to Massachusetts, extending inland to Wisconsin; it is abundant in Essex County, northeastern Massachusetts, where, along the Merrimac River, it reaches the northeastern limit of its continuous range. It then recurs on the estuary of the Nonesuch River, a few miles south of Portland, Maine, and at the mouth of the Kennebec River. Here it is abundant on all parts of the estuary, from fairly saline water to the head of tide. It reaches its eastern limit on the Sheepscot River estuary, a dozen miles east of the Kennebec.

**Zizania aquatica** L., var. **brevis** Fassett (1924b, p. 157). (Pl. 9, fig. 2.) This variety, characterized by its low stature and short-awned lemma, is endemic on the estuary of the St. Lawrence River, about the city of Quebec. The texture of its lemma shows it to be an offshoot, not from the northern var. *angustifolia* Hitchc. (see Fassett, 1924b, p. 157), but from typical *Z. aquatica*, which reaches its northern limits about Lake Champlain and in northern New York. It was probably left long ago as a relic of the retreating *Z. aquatica*, and has been isolated long enough to become varietally distinct. The estuary

of the Kennebec River, on the other hand, is nearer the rest of the range of the Wild Rice, and here this plant has kept the typical form, although on this estuary it does not reach the size attained by this species as it grows farther to the southward.

On the estuary of the Kennebec River there have been collected specimens of *Z. aquatica* which in their small size simulate var. *brevis*, even to the short awn, but they seem to be merely depauperate individuals growing where the water is too saline for their best development, and the short awn is due to the lack of development of the spikelet, as evidenced by the fact that the lemmas are empty; var. *brevis* sets good fruit, still keeping the short awn. However, on the estuary of the Merrimac River, in northern Massachusetts, I have found a few clumps of Wild Rice which have the large habit characteristic of the typical form of the species, and the fruit character of the variety; well-developed spikelets have the awn hardly a centimeter in length.

**Zizania aquatica** L., var. **angustifolia** Hitchc. (1906, p. 210); Fassett (1924b, p. 157). (Pl. 9, fig. 3.) In its lemma character this variety seems closer to var. *interior* Fassett (1924b, p. 158) of the Great Lakes than to typical *Z. aquatica*. It ranges from northern Wisconsin to the eastern boundary of Maine, and has outpost stations on the estuaries of the St. John and the Kennebecasis Rivers. On the Kennebecasis River the Wild Rice is possibly not strictly estuarine. Near Hampton, New Brunswick, where the tidal influence is very slight, the *Zizania* makes an extensive growth in the flooded meadows along the river. The valley of the Kennebecasis River is sheltered and warm, and it may be that the plant has been able to persist on the river shores for a short distance above the estuary.

Some of the plants having outpost stations on the St. John and the Kennebecasis estuaries may prove to have shorter "jumps" than now appear in their ranges, when the territory between the Maine boundary and the St. John River is better known botanically. While eastern Maine has been fairly well botanized, this part of New Brunswick is almost unknown. But even if some of these plants are found between the St. John estuary and Maine, the estuaries will probably remain as the eastern limits for many species.[1]

[1] The report of this plant from Andover, Mass. (Fassett 1927, p. 228), may be incorrect, for the herbarium sheet, from the herbarium of G. U. Hay, of St. John, New Brunswick, does not bear the name Massachusetts. There is an Andover, N. B., on the upper St. John River, near the Maine border.



**Cyperus diandrus** Torr. Widely distributed, from Oklahoma, Nebraska, and Minnesota to Lake Champlain and central Maine, south to Delaware and West Virginia. An isolated station occurs on the estuary of the St. Lawrence River at St. Augustin, Quebec. Brother Marie-Victorin, of the Université de Montréal, is of the opinion that seeds of many plants float down the St. Lawrence River from the Great Lakes, and *C. diandrus* may thus have become established at St. Augustin. On the other hand, it may be a relic of a former wider distribution.

**Cyperus rivularis** Kunth. (Pl. 9, fig. 4.) Across the continent, from California to southern Maine, southward to Virginia and Texas. An outpost station occurs on the St. Lawrence River estuary, just as in the case of *C. diandrus*. In southern Maine the plant is abundant eastward to the valley of the Kennebec River, whence it "jumps" to the estuary of the Penobscot River, where it seems to be a relic.

**Cyperus dentatus** Torr. (Pl. 10, fig. 1.) Northern New York and Delaware to eastern Maine; southwestern Nova Scotia (Fernald, 1922, p. 162); estuaries of the Kennebecasis and the St. John Rivers, New Brunswick. As this species has been found eastward to the valley of the St. Croix River in eastern Maine, it is possible that its occurrence in western New Brunswick may be more general than the present state of our knowledge indicates (cf. *Zizania aquatica*, var. *angustifolia*).

**Scirpus Smithii** Gray. Local from southern New Hampshire (Pease, 1924, p. 37), eastern Massachusetts, and Rhode Island, to northern Indiana (Peattie, 1922, p. 86), southward to New Jersey, where it occurs on the estuary of the Delaware River, and rarely on the coast (B. Long, 1910, p. 156). An outpost station occurs to the northward on the estuary of the St. Lawrence. ("Zone intercotidale de la grève de Beauport, près de Québec," August 8, 1922, Bro. Rolland, No. 15,107, distributed as *S. debilis*.)

**Scirpus Torreyi** Olney. Minnesota to Iowa, eastward to Ottawa and eastern Maine, southward to New Jersey and Pennsylvania. This species reaches the town of Robbinston, on the eastern border of Maine, and is found in an outpost station on the estuary of the St. John River (cf. *Cyperus dentatus* and *Zizania aquatica*, var. *angustifolia*).

**Scirpus fluviatilis** (Torr.) Gray. (Pl. 10, fig. 2.) Across the continent, from California to New York State, reaching the eastern

limit of its continuous range about Lake Champlain. It occurs on the estuaries of the Hudson and the Connecticut Rivers, and extends southward to Chesapeake Bay. Eastward, it formerly grew along the Charles River at Brighton and on the Mystic River estuary at Medford, Mass., until dams were built cutting off the tide from these rivers, and it has been collected on the shores of Heard's Pond, Wayland (Knowlton *et al.*, 1911, p. 84). On the Merrimac River it has been collected at Lawrence and on the estuary at Amesbury, Massachusetts. The only locality for *S. fluviatilis* in Maine is on the estuary of the Kennebec River, where it grows sporadically in patches a few feet across.[1] In New Brunswick it grows only on the estuary of the St. John River, where it makes a solid stand acres in extent at Westfield, and is occasional between Westfield and Fredericton.

It is a puzzling fact that this plant, which along the coast from Massachusetts northward is confined to estuaries, is common along the shores of the St. Lawrence River until it reaches the estuary, where it becomes rare. It is abundant in northern New York and along the St. Lawrence River near Montreal, and extends for some distance below this locality, almost to the head of tide in Lake St. Peter. But below there I have been unable to find it, although it is represented in the herbarium of Mr. Walter Deane by a sheet collected by Macoun at Ste. Anne de Beaupré, perhaps on the tidal shores of the St. Lawrence.

**Juncus acuminatus** Michx. (Pl. 10, fig. 3.) Washington and Oregon; Minnesota to southern Maine, southward to Georgia and Mexico; Nova Scotia (Fernald, 1921–22, p. 242); estuaries from the Kennebec River to Cherryfield, Maine. *J. acuminatus* is found in wet places as far east as Portland, Maine, and thence extends its range eastward on the estuaries of the Kennebec River, the Sheepscot River, the St. George River near Rockland, the Penobscot River, and the Cherryfield River in Washington County, Maine. These may be considered extensions of range to the eastward, in spite of the presence of the plant in Nova Scotia, for Nova Scotia is on a *different line of migration*. In all probability, *J. acuminatus* reached Nova Scotia from the region of Cape Cod, across the now submerged edge of the continental shelf; it is not likely that it could have landed on the estuaries of southern and eastern Maine by this route.

[1] Also reported "near a pond in Perry" by Goodale (1861, p. 128), but it has not been collected in this region since, nor can the specimen be found on which the report was based.



**Nymphozanthus advena** (Ait.) Fernald (1919, p. 186). (Pl. 10, fig. 4.) Nebraska to southeastern New York, southward to North Carolina and Texas (Miller and Standley, 1912, p. 87); southwestern Connecticut (Harger *et al.*, 1917, p. 130); estuary of the Kennebec River, Maine. This "jump" of 250 miles, from the Hudson River to the Kennebec River estuary, is one of the longest made by any estuarine plant.

On the estuary of the Kennebec River this Cow Lily is very abundant and conspicuous, but its distribution there is limited, since it will apparently endure no trace of salinity, and on the other hand is not found as far upstream as the head of tide. Above Richmond (see Pl. 6) it is absent, although *Scirpus Smithii*, var. *levisetus*, *Bidens hyperborea*, var. *cathancensis*, *B. Eatoni*, var. *interstes*, and others, are found at least 15 miles farther up the river. I have been unable to discover the factor which limits the occurrence of this plant.

On the estuary of the Sheepscot River, 10 miles east of that of the Kennebec, *N. variegatus* is abundant, as it is also on the St. John and the Kennebecasis River estuaries, but *N. advena* has been found on an estuarine outpost station only on the Kennebec. On the estuaries south of Connecticut it is, of course, of frequent occurrence.

**Samolus floribundus** HBK. (Pl. 11, fig. 1.) Across the continent, from California to New Brunswick, Nova Scotia, and Prince Edward Island, southward to Florida, the West Indies, and South America. This *Samolus* occurs on the Atlantic coast as far north as Cape Cod, often on brackish marshes, is found inland about Lake Champlain, and extends northeastward on estuaries to eastern New Brunswick, and, apparently as a Coastal Plain migrant, in Nova Scotia and Prince Edward Island. When growing on estuaries it seems usually to prefer rocky shores, and occasionally sheltered clay banks.

The range of this plant is a puzzling one. Should it be classified, perhaps, among the migrants along freshened shores, soon to be discussed, or, indeed, among relics from the unglaciated edge of the continental shelf? Again, on the estuary of the Kennebec River, the *Samolus* is strictly confined to fresh water, but in the following enumeration of stations it will be noted that, especially from Massachusetts southward, it frequently grows in brackish places, or even on salt marshes.

Northeastern part of the range of *Samolus floribundus*.[1]—Connecticut: border of brackish swamp, Stratford; common in salt

[1] Herbarium specimens from all these stations have been seen by the author.

meadows, Orange; "low open pasture near sea shore associated with *Selaginella apus*," Guilford; estuary Hammondasset River, Clinton; estuary Indian River, Clinton; brook by salt marsh, Saybrook. RHODE ISLAND: Newport; brackish marsh, Westerly; Block Island; Field's Point, Providence [probably Corliss Cove, which is brackish]. MASSACHUSETTS: Nantucket; Marthas Vineyard; Hog Island, West Falmouth; Mystic Pond, Medford [once estuarine]; estuary Saugus River; Eastern Point, Gloucester [probably salt marsh]; estuary Ipswich River; estuary Mill Creek, Rowley; estuary Parker River [?], South Byfield; estuary Merrimac River. NEW HAMPSHIRE: Hampton Falls [probably on an estuary]; estuary Salmon Falls River. MAINE: estuary Kennebec River, and other rivers of this estuarine system; estuary Penobscot River. NOVA SCOTIA: estuary Tusket River; estuary Lahave River, Bridgewater; brackish margin of Eel Lake, Yarmouth County; border of salt marsh, Port Clyde; estuary Antigonish River, and neighboring rivers (see page 116 for a discussion of this). NEW BRUNSWICK: estuary Shediac River; estuary Kouchibouguacis River; estuary Kouchibouguac River; estuary Miramichi River. PRINCE EDWARD ISLAND: brackish shore of pond, Selkirk.

**Gentiana clausa** Raf. (see Fernald, 1917d). Indiana to southern Maine, southward to North Carolina and Tennessee. This gentian occurs northeastward to the valley of the Androscoggin River, Maine, and has a very short extension of range on the estuary of the Kennebec River, which is its eastern limit. Here it grows usually just at the limit of high tide where it is never covered deeply, and shows no tolerance of salinity.

**Micranthemum micranthemoides** (Nutt.) Wettst. The range of this species is given by Small (1913, p. 1069, as *Hemianthus*) as on muddy banks from New Jersey to Florida. Its northern limit, in New Jersey, is on the estuary of the Delaware River (Stone, 1911, p. 681), and it also occurs at Salisbury, Maryland (Shreve *et al.*, 1910, p. 480), and in the District of Columbia (Hitchcock and Standley, 1919, p. 251) on estuarine shores.

**Bidens connata** Muhl., var. **fallax** (Warnst.) Sherff (1917, p. 154). *B. connata*, var. *fultior* Fernald & St. John (1915, p. 24). Wisconsin and Minnesota; southeastern Massachusetts, Block Island, and southern Connecticut; estuary of the St. Lawrence River. This appears to be an unimportant variety and its occurrence in an outpost station on the estuary of the St. Lawrence is probably not of great significance.



## PLANTS ALMOST OR ENTIRELY CONFINED TO ESTUARIES.

A number of plants are known which occur only on estuaries. Some of these, such as *Cardamine Longii* of the Kennebec estuary and *Gentiana Victorinii* of the St. Lawrence, are, so far as known, confined to a single estuary, while others, like *Lophotocarpus calycinus*, var. *spongiosus*, are found on almost every estuary from Virginia to the Gulf of St. Lawrence. Although it may be many miles from one estuary to another, the plants of the latter group have bridged the gaps between them. The carriage of seeds from one estuary to another by birds, wind, and ocean currents will at once suggest itself as a possible explanation of this type of disrupted range, but consideration of certain facts shows this method to be an extremely unlikely one. Estuarine plants are of ancient distribution, as evidenced by their development of different varieties on each estuary. *Bidens Eatoni* as found on the Merrimac is different from that of the Connecticut and that of the Kennebec, *Bidens hyperborea* differs markedly on different sections of the coast, while *Lophotocarpus* shows different forms in different parts of its range (see Fassett, 1922). If these plants were spreading to-day by various methods of seed transportation, we should expect to find them uniform on all estuaries. Another factor arguing against this mode of distribution is found in the absence of certain estuarine types from the outer coast of Nova Scotia, parts of Northumberland Strait, and the estuary of the St. John River. The two latter localities lie in the line of migration of estuarine plants, with the same types on either side of them, and have themselves suitable conditions for the growth of these types; if seeds were carried from estuary to estuary, they would certainly have colonized these places. The probable reasons for the lack of estuarine flora in these regions will be discussed presently (pages 111–115).

We are thus led to consider whether the plants now isolated on estuaries could have found their way from river mouth to river mouth at a time when conditions suitable for their growth obtained along the entire coast under discussion, and what factors could have produced these conditions by rendering the water fresh while still tidal.

During the recession of the last ice sheet which covered eastern North America, enormous amounts of fresh water were pouring into the Gulf of Maine. The ice was melting at a rate which produced a great flow of fresh water. "The time occupied by the recession from Hartford [Connecticut] to St. Johnsbury [Vermont] was about 4,100 years. This makes an average rate of about 22 years to a

mile, or of 238 feet (73 meters) a year." (Antevs, 1922, p. 74.) Drainage from the surface augmented this stream.[1] That the water of the Atlantic coast north of Boston was salt or strongly brackish is indicated by the manner of settling of the silt from the glacial streams (Antevs, 1922, p. 3), but this does not preclude the possibility of a strip a few rods wide, freshened on the surface at least, which would have been sufficient for the spread of estuarine plants. There is also a strong possibility that the edge of the continental shelf was not submerged at this time (Fernald, 1911, p. 149–162; Daly, 1920a), and that the brackish sea inside this great barrier would have been a favorable place for the production of estuarine conditions—a sort of Merrymeeting Bay on a large scale (see Pl. 6).

In spite of the recency of the glacial period, the climate at this time was not necessarily frigid.

> The climate was not arctic, for the melting of the ice in many zones was quite rapid. Since, however, a vast amount of heat was used in the melting of the ice and the heating of the cold ice water, the temperature remained comparatively low in a belt off the ice front. This arctic to subarctic zone shifted northward as the ice front withdrew. (Antevs, 1922, p. 89.)

As the ice front was at some distance from the coast, the shores may have been fairly warm.

> We now venture indeed to assume, with G. De Geer, that the melting of the ice was accompanied by a general period of warmth, with widespread change of the earth's absorption of heat. It is clear, however, that during this time the nature of the climate at the edge of the ice was in part, at least, different from what it had been previously. It becomes easy to conceive the beginning of a continental climate with the warm dry summers of the type of the inland of Greenland. (Translated from the German of Nordenskjöld, 1916, p. 45, and referring to conditions in Scandinavia.)

Exactly at what stage during the retreat of the ice sheet the estuarine plants migrated along the coast, it is hard to say. The glacier was probably many miles from the coast, so that the cooling effect was not very strong along the shore.

Much of the coast from Boston northeastward was submerged at this time (De Geer, 1892; Chalmers, 1905; Sears, 1905, p. 272–273; Katz and Keith, 1917, p. 26–27; Katz, 1918a, 1918b; Goldthwait,

[1] In this connection, the late Professor J. B. Woodworth once pointed out to me that the drainage at this time came from the surface of the great ice sheet, probably including rainfall from as far north as Hudson Bay, as contrasted with the present rather limited watersheds of the rivers from Nova Scotia to Virginia.



1920; Daly, 1920a, 1920b; Antevs, 1922, fig. 6; Churchill, 1923; Shaler *et al.*, 1896, p. 994). The Isthmus of Chignecto was under the sea and the water flowed from the present Bay of Fundy to the Gulf of St. Lawrence, as is shown in Plate 8 (see Chalmers, 1895, p. 19; Ganong, 1903, p. 167). This submergence contributed indirectly to the warmth of the water. Professor H. B. Bigelow has shown that the present cool climate about the Bay of Fundy and the Gulf of Maine is due, not to the Labrador Current, but to the fact that the enormous tides of the Bay of Fundy have a stirring effect, bringing up cold water from the depths. The water of the Bay of Fundy is at an almost constant cold temperature at all depths, while southward the surface water is warmer, and the deep water cooler, than that of the Bay. That this condition is due to mixing of the water is also indicated by the fact that the salinity of the Bay is more nearly constant at different depths than is that of the water farther south (Bigelow, 1914, p. 88–98). About the south shore of the Gulf of St. Lawrence, from Northumberland Strait to Chaleur Bay, the summers are mild; in the warm water thrive some 28 species of marine invertebrates of Carolinian waters (Ganong, 1891) and along the shores are plants of otherwise southern distribution (Blake, 1918). This is because the water is shallow, and the tide is not great, ranging from 1.8 to 4.2 feet in Northumberland Strait, and to 8 feet in Chaleur Bay. When the Isthmus of Chignecto was submerged, the water ran freely from the Gulf of Maine to the Gulf of St. Lawrence, and the funnel effect which causes the exaggerated tides in the Bay of Fundy was not present (Chalmers, 1895, p. 19), so that the calm warm conditions of Chaleur Bay extended along the entire coast.

Thus it appears that the conditions now found only on estuaries extended at one time (although probably not all at the same time) from the St. Lawrence River southward to Boston. As regards the coast south of Boston, Woodworth (1896, p. 167–168; 1897, p. 108–109; 1905, p. 229–234) finds no evidence of submergence, and Antevs (1922, p. 5) sees good reason to believe that while the ice sheet was disappearing, southern New England stood at a higher level than at present. But the elevation of the land at that time, whether greater or less than at present, would have had little bearing on the estuarine character of the shores; it would have affected the position of these shores only. Although the glacier did not extend southward as far as Chesapeake Bay, the fresh water from its melting may well have influenced the character of the sea as far south as there. And it is to Chesapeake Bay that the estuarine flora extends.

Along the shores from Chesapeake Bay to the Gulf of St. Lawrence, then, in a belt following the retreating ice border, there seems to have been in late glacial times a tide in fresh or slightly brackish water, now found only at the mouths of rivers. Here a new flora arose, consisting of plants which adapted themselves to these conditions.

Dr. Antevs, who has been most helpful in offering suggestions and criticisms of this hypothesis, is of the opinion that when the glacier was near enough to the coast to reduce the salinity of the sea, the water must necessarily have remained rather cold. But just because estuaries are warm to-day and their warmth favors the growth of some species, we may not assume that they have always been so. In the consideration of species following, it will be seen that only two plants are of southern affinity. In fact, *Bidens hyperborea* reaches Hudson Bay, and the relatives of the other estuarine species, when known, are found to be plants of the north temperate regions. Fresh tidewater, not mild temperature, seems to be the ruling factor in this case. The two plants of southern affinity are *Lophotocarpus calycinus*, var. *spongiosus*, and *Lilaeopsis lineata* (see Pl. 13, figs. 1, 3), which grow in brackish water (see page 82). As the influx from the melting glacier decreased and the sea became more brackish, the species of cool fresh water were confined to those places where the water remained fresh, i. e., to the mouths of rivers. Dr. Antevs agrees with me that as the water became more brackish it probably became warmer, for the edge of the ice sheet was then much farther away. Then *Lophotocarpus* and *Lilaeopsis* thrived along the shores. As the water became even more saline, these in their turn were confined to estuaries, and *Ruppia*, *Zannichellia*, and various mollusks of warm brackish water (see Ganong, 1891) took their place. Finally the shores became populated entirely with plants of the salt marsh, then the Isthmus of Chignecto rose, closing the head of the Bay of Fundy, and conditions became as they are today.

The presence of certain salt-marsh species, of southern affinity, in northeastern New Brunswick (see Blake, 1918) would indicate that not until the water had become nearly as saline as it is now was the connection between the Bay of Fundy and the Gulf of St. Lawrence closed.

Professor Fernald (1924) has pointed out that the Coastal Plain flora isolated in Nova Scotia contains only one endemic species which may or may not have originated there. From the facts just



discussed, it seems probable that the estuarine plants spread along the shores at approximately the same time that the Coastal Plain migration took place, or perhaps much later,[1] but there are species which are restricted to estuaries, which must therefore have originated presumably since the migration of the plants of the Coastal Plain to Nova Scotia. Apparently because of the extreme conditions under which they grew, the plants of estuarine shores have evolved more rapidly than have those derived from the Coastal Plain and isolated in Nova Scotia.

**Isoëtes saccharata** Engelm. (Pl. 12, fig. 1.) Confined to the estuaries of rivers entering Chesapeake Bay. See Shull (1903) and Pfeiffer (1922, p. 179) for complete discussions of this range.

**Lophotocarpus calycinus** (Engelm.) J. G. Smith, var. **spongiosus** (Engelm.) Fassett (1922, p. 73). (Pl. 11, fig. 2; Pl. 13, fig. 1.) The genus *Lophotocarpus* is primarily one of the equatorial regions and the southern hemisphere. It has representatives in tropical Africa, Madagascar, India, Sumatra, Java, and northern Australia. In the western hemisphere it occurs throughout northeastern South America, Central America, and eastern Mexico, while *L. calycinus* is widely distributed in the Mississippi Valley and reaches the Atlantic coast in Maryland and Delaware. The typical form of the plant has hastate leaves, but lanceolate leaves occasionally occur, just as in the case of *Sagittaria latifolia*. Var. *spongiosus* is found on estuaries from Maryland to New Brunswick, and is smaller than the typical form of the species. The geographic forms of this variety have been described elsewhere (Fassett, 1922).

Of all the estuarine plants, this *Lophotocarpus* is one of the most tolerant of salinity, but I have not been able to determine the maximum or minimum which it can endure. The most brackish water in which I have found it was on the Miramichi River, five miles above Newcastle, New Brunswick, where the water left standing about it

[1] Fernald (1911, p. 149–162) has hypothesized that plants of the Coastal Plain reached Nova Scotia and Newfoundland by migration over the now submerged continental shelf in postglacial times. Johnson and Stolfus (1924) have shown that the continental shelf stood higher in preglacial times than at present, while Moon and Bray (1925) have demonstrated that the edge of the continental shelf is now at progressively greater depths as it is followed northward, indicating a depression of the northern end. The theory that this migration occurred in preglacial times is considered by Professor D. W. Johnson (1925, p. 303), who quotes a letter from Fernald entertaining this possibility.

at low tide was about 22 per cent as saline as that of the ocean. It is evident that a great many tests of water at different depths and at all conditions of tide must be made before we can learn the tolerance of this plant on one estuary alone, and it is possible that the strains on the different rivers may act differently.

The fact that the *Lophotocarpus* is sometimes found growing with *Spartina alterniflora* should not be taken as indicative of a salt-marsh habitat for the former plant; the latter has simply adapted itself to less salinity than it usually gets. (For tolerance of fresh water by halophytes, see Osterhout, 1906, 1917.)

North of the Miramichi River, New Brunswick, *Lophotocarpus calycinus*, var. *spongiosus*, is absent, nor is it found at the mouths of the rivers entering the Bay of Fundy. It has been reported (Fowler, 1885, p. 67, as *Sagittaria calycina*, var. *spongiosa*) from the head of tide in the Richibucto River, from Rothesay, and from the Tobique River, all in New Brunswick. The Tobique is a tributary to the upper St. John River, and so has no estuary; Professor Fernald has seen the specimen upon which this report was based, and says that it is not a *Lophotocarpus*. On two occasions I have collected along the tidal shores of the Kennebecasis River at Rothesay in an attempt to corroborate the report of the occurrence of this plant there, but without success. However, *Sagittaria graminea*, often simulating *Lophotocarpus*, is present. I was also unable to find *Lophotocarpus* on the neighboring estuary of the St. John River, although I searched the shores at Westfield, where conditions of salinity seemed proper for the plant.

Range of *Lophotocarpus calycinus*, var. *spongiosus*.[1]—Delaware: estuary Delaware River. New Jersey: estuary Delaware River; estuary Hackensack River. New York: estuary Hudson River House, 1924, p. 62). Connecticut: estuary Housatonic River; estuary Connecticut River; estuary Ash Creek, Bridgeport; estuary Indian River, Clinton. Massachusetts: estuary Mystic River (station probably extinct since the damming of the river at Medford); estuary Saugus River; estuary Mill Creek, Rowley; estuary Merrimac River. New Hampshire: estuary Salmon Falls River. Maine: estuary Mousam River, Kennebunk; estuary Kennebec River, and other rivers of this estuarine system; estuary Sheepscot River; estuary St. George River, Warren; estuary Penobscot River. New

[1] Herbarium specimens representing each station have been examined, except where references are given.



Brunswick: estuary Buctouche River; estuary Richibucto River; estuary Kouchibouguacis River; estuary Kouchibouguac River; estuary Miramichi River; estuary Moulies River.

**Eleocharis diandra** C. Wright. This is a species of very local distribution, occurring usually on river gravels and sandy shores, occasionally on estuaries. It was first described from silts along the Connecticut River, and has since been found on the shores of Oneida Lake, N. Y. (Burnham, 1919, p. 126; House, 1924, p. 137), about Lake Champlain, on the Hudson River at Baker's Falls (House, 1924, p. 137), and on the shores of Lake Ossipee, N. H. (Pease, 1924). The estuarine stations for this plant are on the Hudson (Svenson, 1925, p. 222), the Connecticut, and the Kennebec Rivers. Since *E. diandra* is on the shores of two of these rivers above the estuaries, it is perhaps to be looked for on the upper Kennebec.

**Scirpus Smithii** Gray, var. **levisetus** Fassett (1921a, p. 42). This sedge occurs only on the estuaries of the Kennebec and the St. Lawrence Rivers. On the Kennebec it is abundant from a short distance above Bath to Gardiner, near the head of tide. On the St. Lawrence it has been collected but twice, at St. Augustin and Levis.

Whether this variety once grew continuously from the St. Lawrence to the Kennebec, or has arisen independently on the two estuaries, is a question which will admit of some speculation. Collections from the St. Lawrence seem to be identical with those from the Kennebec.

**Eriocaulon Parkeri** Robinson. (Pl. 11, fig. 3.) Confined to estuaries from Virginia to Maine. Professor Robinson stated that this species seemed to be derived from the southern *E. Ravenelli*, but Professor Fernald, who has recently examined it, has come to the conclusion that it is more nearly related to *E. septangulare*, since its seeds seem identical with those of the latter species. Indeed, *E. Parkeri* is doubtfully distinct from *E. septangulare*, and is perhaps no more than an ecological form. (See also Pennell, 1924, p. 11.)

Range of *Eriocaulon Parkeri*.—Virginia: estuary Chickahominy River; estuary Potomac River. New Jersey: estuary Delaware River; estuary Maurice River. Delaware: estuary Delaware River. Connecticut: estuary Housatonic River; estuary Quinnipiac River, North Haven; estuary Indian River, Clinton; estuary Pocough (or Patchogue) River, Westbrook; estuary Connecticut River.

MASSACHUSETTS: estuary Taunton River; estuary Merrimac River. MAINE: estuary Nonesuch River, Scarboro; estuary Kennebec River, and other rivers of this estuarine system; estuary Sheepscot River; estuary Penobscot River.

**Cardamine Longii** Fernald (1917b). Endemic on the estuarine system at the mouth of the Kennebec River, Maine. This species has been found in only two or three patches on the Cathance River estuary (see Pl. 6) and in one on the shores of Merrymeeting Bay, where sheltered by ledges or the overhanging branches of trees. "In the type locality the plant was in the shadow of an overhanging ledge" (Fernald, 1917b). I have looked for this species in many apparently appropriate places on the Kennebec River and on the shores of Merrymeeting Bay, as well as on other estuaries, but, although *C. pensylvanica* was often present, no more *C. Longii* was to be found.

On the shores of the Charles River near Newton Upper Falls, Mass., *C. Longii* has been grown from seed planted by Mr. F. F. Forbes.

**Elatine americana** (Pursh) Arnott. (Pl. 11, fig. 4.) Fernald (1917a) has demonstrated that the common *Elatine* of eastern North America is *E. minima* (Nutt.) Fisch. & Meyer, while the true *E. americana* is almost entirely restricted to estuaries, being reported from that of the Kennebec system, from the Delaware River estuary and the shore of a neighboring pond, from several pond shores in southern Connecticut, and from the shore of the Ottawa River at Hull, Quebec. Since the publication of Fernald's paper, the plant has been found on the estuaries of several other rivers.

The occurrence of a normally estuarine species in nonestuarine habitats may be easily explained. At the time when estuarine conditions obtained generally along the coast, the land was somewhat submerged, which means that the present locations of many estuaries were covered by deep water, and the estuaries were farther up the streams. The estuary corresponding to that now existing at the mouth of the St. Lawrence was then extending along the upper St. Lawrence and Ottawa Rivers, probably as far, at least, as the present location of Hull and Ottawa. As the land rose, estuarine conditions moved downstream, and the plants of course followed these conditions. But *Elatine americana* found favorable conditions and persisted at Hull. The ponds in Connecticut about which this species



grows are near estuaries which also harbor it, and it is possible that these ponds and estuaries were once connected.

On the other hand, there is the possibility of a once general distribution of a plant having such a range, and a subsequent dying out except in a few places, of which some were estuaries.

Range of *Elatine americana*.—QUEBEC: on mud of Ottawa River, Hull. NEW BRUNSWICK: estuary Miramichi River; estuary St. John River; estuary Kennebecasis River. MAINE: estuary Kennebec River, and other estuaries of this system; estuary Nonesuch River, Scarboro. CONNECTICUT: muddy pond shores, Southington; muddy pond shore, Orange; muddy pond shore, Huntington; estuary Indian River, Clinton. NEW YORK: estuary Hudson River. NEW JERSEY: estuary Delaware River. PENNSYLVANIA: estuary Delaware River. DELAWARE: estuary Brandywine Creek; pond shore, Middletown.

**Epilobium glandulosum** Lehm., var. **ecomosum** Fassett (1924a). The occurrence of this variety on the estuary of the St. Lawrence River has been discussed on page 85. On the Harrington River in eastern Maine, *E. glandulosum*, var. *adenocaulon*, grows where submerged at high tide and is often heavily coated with mud, but here the seeds retain the coma. Brother Marie-Victorin tells me that he has grown this plant, and that it has remained constant through two generations.

**Lilaeopsis lineata** (Michx.) Greene. (Pl. 12, fig. 1; Pl. 13, fig. 3.) This plant is somewhat comparable to *Lophotocarpus calycinus*, var. *spongiosus*, both in the distribution of the genus, and in the degree of salinity which it prefers. The genus *Lilaeopsis* occurs in southern Australia, New Zealand, South America, and western North America, while *L. lineata* ranges from Nova Scotia (Fernald, 1921–22, p. 110) to Florida, on the more saline parts of estuaries; in fact, it often grows intermixed with *Spartina alterniflora*, but probably never in pure sea water. It seems perhaps a little more tolerant of salinity than is its neighbor *Lophotocarpus*. On the shore of Cape Cod, where the land is springy and a large quantity of fresh water enters the ocean, the *Lilaeopsis* occurs, although there are no true estuaries. This is one of the few estuarine plants which grow as such in Nova Scotia.

Range of *Lilaeopsis lineata*.—NOVA SCOTIA: estuary Tusket River. MAINE: estuary Kennebec River. NEW HAMPSHIRE: estuary Salmon Falls River; estuary Lamprey River, Newmarket; estuary Swampscot

River, Exeter (Eaton, 1900, p. 168). MASSACHUSETTS: estuary Mill Creek, Rowley; estuary Ipswich River; estuary Neponset River, Milton; brackish marshes, Wareham; estuary Bass River, Yarmouth; salt marsh, Barnstable; brackish marsh, Bourne; estuary Taunton River. RHODE ISLAND: estuary Seekonk River. CONNECTICUT: estuary Connecticut River; estuary Indian River, Clinton; estuary Housatonic River; salt meadows, East Haven. NEW YORK: estuary Hudson River (House, 1924, p. 535); salt meadows, Wading River, Long Island (House, 1924, p. 535). NEW JERSEY: Barnegat Bay—"at Palermo the little plants were creeping over the white sand of a slight depression where a fresh water spring bursts forth near the edge of the salt marsh" (Stone, 1911, p. 599); near Egg Harbor (Stone, 1911, p. 599). MARYLAND: estuary Little Gunpowder Creek; "confined to shallow water and tidal flats in the brackish and fresh water of the upper Chesapeake and its tributaries: frequent" (Shreve *et al.*, 1910, p. 462). VIRGINIA: tidal marsh, Capitol Landing; Queen's Creek, north of Williamsburg (Grimes, 1922, p. 151). NORTH CAROLINA: eastern part of the state, no definite locality given. FLORIDA: Jacksonville.

**Bidens bidentoides** (Nutt.) Britton. (Pl. 12, fig. 2.) This is a strictly estuarine species, occurring on the Susquehanna River (Stone, 1911, p. 773), the Delaware River, the Maurice River of southern New Jersey, and the Hudson River (Svenson, 1925, p. 221) estuaries. A report of this species from the District of Columbia (Hitchcock and Standley, 1919, p. 289) seems to have been founded on a specimen of *B. connata* Muhl., var. *anomala* Farwell.

**Bidens Eatoni** Fernald. (Pl. 12, fig. 3.) *B. Eatoni*, var. *typica* Fassett: endemic on the estuary of the Merrimac River. *B. Eatoni*, var. *fallax* Fernald: also on the estuary of the Merrimac River. *B. Eatoni*, var. *interstes* Fassett: on the estuaries of the Kennebec and the Sheepscot Rivers, Maine. *B. Eatoni*, var. *mutabilis* Fassett: endemic on the estuary of the Kennebec River. *B. Eatoni*, var. *kennebecensis* Fernald: endemic on the estuarine system at the mouth of the Kennebec River, and rare on the estuary of the Merrimac River. *B. Eatoni*, var. *simulans* Fassett: endemic on the estuary of the Connecticut River. *B. Eatoni*, var. *major* Fassett: estuaries of the Quinnipiac River, North Haven, Conn., and of the Hudson River. (See Fassett, 1925b, for a taxonomic treatment of these varieties.)



× **Bidens multiceps** Fassett (1925b, p. 145). Endemic on the estuary of the Taunton River, Mass. This plant is tentatively treated as a hybrid of *B. connata* and *B. Eatoni*, although the latter plant has not been found on the Taunton River estuary.

**Bidens hyperborea** Greene. (Pl. 12, fig. 2.) The treatment of this variable species by the present writer (1925c) can be regarded only as tentative. Var. *typica* Fassett came from Rupert House, James Bay, Canada, and is described as being simple and monocephalous, with entire or few-toothed leaves. Plants matching this description were collected by Svenson and Fassett on the estuary of the Restigouche River, New Brunswick; this collection is cited (Fassett, 1925c) as No. 889 under var. *laurentiana*. The unbranched plants with small achenes formed colonies distinct from those of the larger variety also present on this estuary, and were considered in 1925 to be mere dwarfed forms of it. This is probably the case, but it is possible that the type collection from James Bay, the only collection known, may represent small forms of a larger plant present on the estuaries of rivers entering Hudson Bay. The final word may not be spoken until complete collections have been made in that region.

*B. hyperborea*, var. *colpophila* (Fernald & St. John) Fernald, seems to occur on estuaries from Northumberland Strait to northern Massachusetts. It appears to consist of several localized races. *B. hyperborea*, var. *cathancensis* Fernald, has a more restricted range, on the estuarine system at the mouth of the Kennebec River, Maine. Certain plants on this estuary, where var. *colpophila* is also found, seem to take on the character of both varieties, having the small achenes of var. *colpophila* and the narrow involucral bracts of var. *cathancensis*.

*B. hyperborea*, var. *laurentiana* Fassett, was described from the estuary of the St. Lawrence River, Quebec. A large series of plants, from Chaleur Bay to Northumberland Strait, New Brunswick, collected in August, 1923, by Svenson and Fassett, are referred to this variety, but are so young that their character cannot be definitely determined. Perhaps collections of better material will prove them to belong nearer var. *arcuans* Fernald, at present known only from the type collection on the estuary of the Miramichi River, New Brunswick.

*B. hyperborea*, var. *gaspensis* Fernald, is found on the estuaries of the St. John and the Dartmouth Rivers, Gaspé County, Quebec, while

var. *Svensoni* Fassett, from the Rimouski River, Quebec, is closely related to it, but far from identical with it.

Mr. E. E. Sherff has kindly sent me a specimen of a *Bidens*, collected on July 15, 1827, on the Hackensack marshes, New Jersey. It is *B. hyperborea*, in a form close to var. *laurentiana*, with large achenes 8.5 mm. long, and long involucral bracts. This sheet is from the herbarium of M. J. Hennecart, now in the Herbarium of the Paris Museum.

**Bidens cernua × hyperborea** Fassett (1925c, p. 171). Found only on the estuary of the Nonesuch River, Scarboro, Maine, this plant combines the characters of its two supposed parents.

**Bidens frondosa** L., var. **anomala** Porter. On estuaries and brackish shores, and occasionally inland. Range.—QUEBEC: estuary St. Lawrence River. NEW BRUNSWICK: estuary Restigouche River; estuary Kennebecasis River. NOVA SCOTIA: brackish shores, St. Ann, Cape Breton Island; brackish shores, Halifax; "in *Zostera* litter, gravelly sea-beach, Yarmouth Bar; margin of thicket bordering cobbly beach of Parr Lake; the latter station unusual in being on a fresh-water lake, the variety usually occurring in brackish habitats" (Fernald, 1922, p. 207). MAINE: cobblestone beach, Bar Harbor (Fassett, 1927); cobblestone beach, Ocean Point (Fassett, 1925a, p. 56); rocks along the shore, Squirrel Island; estuary Androscoggin River (Fernald, 1913, p. 75); brackish shore, Woolwich. MASSACHUSETTS: shingle beach, Hull (Blake, 1925); brackish shores, Cape Cod. PENNSYLVANIA, NEW JERSEY, and DELAWARE: estuary Delaware River. DISTRICT OF COLUMBIA: estuary Potomac River. MARYLAND: banks of the Chesapeake and Ohio Canal, between Locks 10 and 12, near Cabin John (Blake, 1925). NEW YORK: Chaumont; shores of Black Lake (these two collections, *Fernald, Wiegand*, and *Eames*, Nos. 14492 and 14494, were distributed as *B. discoidea*). Also reported from the sand hills of KANSAS and NEBRASKA (Sherff, 1917, p. 34).

Although this variety has been reported from the estuary of the Androscoggin River, I do not believe that it is characteristically an estuarine plant in this region. I have not found it on this estuarine system, but have collected it near the estuary at Woolwich, where it grew on a stony shore, just above high-tide level. Here the water is salt (see Pl. 6).



RELICS FROM THE CONTINENTAL SHELF.

A few species, European or Cordilleran in their affinities, appear to have survived the last glaciation on the unglaciated edge of the continental shelf, and are found at present on land neighboring the now submerged edge of this shelf, and on estuaries.

**Tillaea aquatica** L. (Pl. 12, fig. 4; Pl. 13, fig. 2.) Northern Europe, Iceland, Spitzbergen, eastern Siberia, Japan; western North America from Montana and northern California to Mexico and eastern Texas; the Atlantic coast of North America from the estuary of the St. Lawrence River and southeastern Newfoundland to Maryland.

Range of *Tillaea aquatica* in northeastern North America.—NEWFOUNDLAND: Argentia, Avalon Peninsula. QUEBEC: wet brackish sand, Grindstone Island, Magdalen Islands; estuary St. Lawrence River. PRINCE EDWARD ISLAND: wet brackish sand, Tracadie. NEW BRUNSWICK: estuary Miramichi River; estuary Kouchibouguac River; estuary Kouchibouguacis River. NOVA SCOTIA: fresh-water pond, Sable Island; damp sand, Villagedale. MAINE: estuary Penobscot River; estuary Kennebec River, and other rivers of this estuarine system. MASSACHUSETTS: estuary Merrimac River; brackish pond shores, Nantucket. CONNECTICUT: estuary Mill River, New Haven. NEW YORK: estuary Hudson River (House, 1924, p. 375). MARYLAND: estuary Wicomico River.

**Gentiana Victorinii** Fernald (1923). Endemic on the estuary of the St. Lawrence River. This species appears to be of the same stock as *G. nesophila* of Newfoundland, Anticosti, and the Mingan Islands.

**Limosella subulata** Ives (see Fernald, 1918b, and Pennell, 1919). (Pl. 12, fig. 4.) The genus *Limosella* is circumpolar in both the northern and the southern hemispheres. The *L. aquatica* of Europe is in eastern North America found only on the south coasts of the Labrador Peninsula and Newfoundland, while *L. subulata*, which Professor Fernald has shown to be specifically distinct from it, occurs on estuaries. It also has to some extent an insular occurrence which indicates some migration over the now submerged continental shelf, possible in preglacial times (see Johnson and Stolfus, 1924). Since it has no relatives immediately to the southward or to the westward of its range, but seems to center about the unglaciated edge

of the continental shelf, *L. subulata* may be classed with *Tillaea aquatica*, as an apparent relic of the preglacial flora which has found estuarine conditions favorable for its existence.

*L. subulata* may grow on a sandy shore where the water that periodically covers it is perfectly fresh, or it may exist where the water is only a little less saline than that in which *Lophotocarpus* flourishes. In habit and size it is also variable, for it may form a dense turf or it may occur as scattered plants a few centimeters apart and connected by fragile runners. The leaves vary from threadlike to a millimeter or more in thickness.

Range of *Limosella subulata*.—NEWFOUNDLAND: salt marsh and brackish mud, Norris Arm; muddy shores and brackish pools, Carbonear. QUEBEC: estuary St. Lawrence River; estuary Rimouski River; estuary Dartmouth River; estuary Bonaventure River; brackish muddy shore, New Carlisle; wet brackish sands, Magdalen Islands. PRINCE EDWARD ISLAND: brackish mud, Tignish; wet brackish sand, North Lake; Brackley Point; wet brackish sand, Grand Tracadie; wet sand, Britain Pond. NEW BRUNSWICK: estuary Miramichi River; estuary Nipisiguit River, Bathurst; estuary Kouchibouguacis River; estuary Tracadie River; estuary Buctouche River; estuary Shediac River. NOVA SCOTIA: estuary River Philip; estuary Shinimikas River; brackish shore, Sidney Mines, Cape Breton Island; damp sand-flats, Villagedale; estuary Tusket River; brackish sand, Sable Island. MAINE: estuary Union River; estuary Penobscot River; estuary St. George River, Warren; estuary Sheepscot River; estuary Kennebec River, and other rivers of this estuarine system. NEW HAMPSHIRE: estuary Salmon Falls River. MASSACHUSETTS: estuary Merrimac River; estuary Mill Creek, Rowley; estuary Ipswich River; Plymouth; sandy pond margins, Cape Cod; pond shores, Marthas Vineyard; shallow water, Nantucket. RHODE ISLAND: pond shores, Block Island; Little Compton. CONNECTICUT: estuary Beaver Creek, Milford; shores of Lake Saltonstall, Branford (Harger *et al.*, 1917, p. 248); estuary Quinnipiac River, New Haven. NEW YORK: Fishers Island; estuary Hudson River (House, 1924, p. 623); Fort Pond Bay, Long Island (House, 1924, p. 623). NEW JERSEY: estuary Hackensack River; pond margin, Point Pleasant; estuary Delaware River; "edges of salt marshes from Long Beach to St. Albans" (Stone, 1911, p. 681). MARYLAND: Lloyd's Creek, Kent County (Shreve *et al.*, 1910, p. 480).



PLANTS MODIFIED BY ESTUARINE CONDITIONS.

**Leersia oryzoides** (L.) Sw., forma **glabra** A. A. Eaton (1903). This form, already discussed on page 85, was described by Eaton from the estuary of the Merrimac River. He attributed its smoothness to the fact that it was submerged twice a day by fresh water. This view was strengthened when he found a patch of *L. oryzoides* which was partly above, partly below, the high-tide level; the part which grew above the inundated shores consisted of the typical form of the species, while that which was covered at high tide was forma *glabra*.

This form also occurs on the estuary of the Kennebec River, and is approached by collections from Trefry's Lake, Nova Scotia (Fernald, 1921–22, p. 229).

**Myrica Gale** L. This shrub is not characteristic of estuaries, but a single specimen collected by Fernald and Long on the tidal flats of the Cathance River, in the Kennebec River estuarine system, shows reaction to its environment in the development of short, thick, coriaceous leaves.

**Polygonum sagittatum** L., forma **chloranthum** Fernald (1917a, p. 134). Common on the estuary of the Kennebec River, and also found on those of the Merrimac and Connecticut Rivers. Although this is usually an estuarine form, green-flowered plants may occur elsewhere; I have found them in damp places at Ocean Point, Maine, and in some parts of northern Wisconsin. These specimens lack the habit which is ordinarily characteristic of this form, and which is probably a direct result of frequent submergence, for the estuarine plant has not only the green flowers indicated by the name, but slender stems and weak prickles.

**Sium suave** Walt., forma **fasciculatum** Fassett (1921b). (Discussed on page 84.) This form occurs frequently on the estuary of the Kennebec and that of the neighboring Sheepscot River. I also collected it on the muddy shore of Shirley Reservoir in Shirley, Mass., in September, 1921; the summer was very dry that year, and the plant was growing where it had been under water earlier in the season. *S. suave*, forma *fasciculatum*, was found on September 16, 1915, at the edge of a pond in Norton, Mass., by Mr. F. W. Hunnewell, who tells me that it grew on the shore left exposed by the drying of the pond. The specimen is now in Mr. Hunnewell's herbarium.

**Lycopus uniflorus** Michx., forma **flagellaris** Fernald (1921–22, p. 289). Known only from the type station on a lake margin in North Sidney, Nova Scotia, and from one plant collected at Bowdoinham, Maine, on the estuary of the Cathance River. In the latter locality its occurrence is probably due to periodic submergence.

**Aster puniceus** L., var. **firmus** (Nees) T. & G., forma **rufescens** Fassett (1925d). This form, having the leaves dark red above, has been collected but once, by Bro. Marie-Victorin, who found a large patch of it on the estuary of the St. Lawrence River.

## ESTUARINE CONDITIONS ALONG THE NEW ENGLAND COAST.

On the western half of the Connecticut coast, the tide ranges from 4.5 to 8.7 feet (U. S. Coast and Geodetic Survey, 1923, p. 350), and collecting on the river mouths is productive of estuarine plants. The Connecticut and the Housatonic Rivers have large estuaries which are still in need of thorough botanizing. The small streams between Saybrook and New Haven often harbor *Lophotocarpus*, *Eriocaulon Parkeri*, and *Samolus*, while *Lilaeopsis* is frequent in the more brackish places. The Quinnipiac River, which enters Long Island Sound at New Haven, is especially promising. The estuary of this river is at North Haven, six miles above New Haven, and here are great areas of *Typha angustifolia* and *Zizania aquatica*, mixed with *Bidens Eatoni*, var. *major*, *Limosella subulata*, and *Eriocaulon Parkeri*. *Lophotocarpus* and *Lilaeopsis* should be sought on the more brackish parts of this estuary.

East of the Connecticut River, conditions are not so promising. The city of Norwich has been built on the estuary of the Thames, and factories and sewage have destroyed any estuarine plants which may once have been there, while from the mouth of the Thames to Narragansett Bay the tide ranges only from 2.5 to 3.8 feet (U. S. Coast and Geodetic Survey, 1923, p. 349), an amount insufficient to produce large estuaries. On the Pawcatuck River, the boundary between Connecticut and Rhode Island, there is only a very short extent of estuarine shore and no estuarine plants have been found there.

The islands south of Connecticut and Massachusetts, although lacking rivers, harbor a few estuarine species; this is also true of Cape Cod, where the sea water is somewhat diluted by springs along the coast (see *Tillaea aquatica*, *Lilaeopsis lineata*, *Samolus floribundus*, and *Limosella subulata* in the discussion of species).



The estuary of the Taunton River is worthy of further exploration; on it have been found *Bidens multiceps*, *Lilaeopsis lineata*, and *Eriocaulon Parkeri*.

About Boston several estuaries once existed, but they have been obliterated by the expansion of the city. On the Charles River the tide formerly extended to Watertown, and salt-marsh types are found today at Mount Auburn. That the water was brackish about Watertown Arsenal is indicated by a report of *Zannichellia* from there (Deane, 1910), and there is in the Gray Herbarium an old sheet of *Scirpus fluviatilis* collected at Brighton, perhaps on tidal shores. The building of the dam in 1908 cut off the tide from the Charles River, and its estuary is no longer in existence; we can only surmise what its flora may have been. The Mystic River, too, was once estuarine, and the tide extended throughout the Mystic Lakes and up Alewife Brook to Fresh Pond; from this estuary, now destroyed, like that of the Charles, by a dam, we have old collections of *Lophotocarpus* and *Samolus*. The only estuary now existing in the vicinity of Boston is that of the Saugus River, near Lynn, where grow *Lophotocarpus* and *Samolus*.

While many streams enter the ocean about Salem, Beverly, and Danvers, they are all too small to have estuaries. A day of searching in this vicinity yielded no estuarine plants.

North of Cape Ann is the estuary of the Ipswich River, largely spoiled by factories along its bank, but with *Limosella* and *Lilaeopsis*. The former has not been collected there for many years, and I was unable to find it in October, 1922. It may be that, since it usually prefers fresher water than does *Lilaeopsis*, it once grew on that part of the estuary which is now occupied by factories, while the latter, in more brackish water and hence nearer the ocean, has not been so disturbed.

The most extensive estuary in Massachusetts is that of the Merrimac, where grow *Lophotocarpus*, *Scirpus fluviatilis*, *Tillaea*, *Bidens Eatoni*, *B. hyperborea*, *Eriocaulon Parkeri*, and *Samolus floribundus*, while on the near-by Parker River and its tributary, Mill Creek, many of these types also occur. Extensive collecting will probably yield more interesting forms from this region.

The coast of New Hampshire is short, but has several rivers which are worthy of exploration. The Salmon Falls River has a good quota of estuarine plants; *Lilaeopsis* has been collected at Newmarket, and it is probable that there are many good estuaries in this region.

Between Kittery, Maine, and Portland, there are several river mouths which may repay attention. The Saco, the largest of these, has been dammed at its mouth, but *Bidens hyperborea* and *Lophotocarpus* have been collected on the Mousam River at Kennebunk, while the *Bidens*, *Zizania aquatica*, and the rare *Elatine americana* have been found by Mr. A. H. Norton on the Nonesuch River, at Scarboro. Northeast of Portland is the Royal River, which has been dammed at Yarmouth. A few miles farther up the coast is the largest estuary in Maine, that of the Kennebec River, which is confluent with those of the Androscoggin, Cathance, Muddy, Abagadasset, and Eastern Rivers; while so close that their floras have undoubtedly been derived from this system are the smaller Winnegance and Back River Creeks, the former well known through the collecting of Miss Kate Furbish.

On this estuarine system there are three varieties of *Bidens Eatoni* and two of *B. hyperborea*. This wealth of forms is probably due to the fact that at the time when the plants became isolated on river mouths, the land was lower than it is now, and Merrymeeting Bay (see Pl. 6) was salt, so that the estuaries of the Kennebec and the Androscoggin were farther up the rivers, and separate. On these estuaries different varieties arose by long isolation. As the land rose, the estuaries moved down stream until they became confluent in Merrymeeting Bay, and the varieties mingled, perhaps hybridized, and produced the complexity found in this region today.

The estuaries of Winnegance and Back River Creeks are comparatively young, for the streams are very short and at the time when estuarine floras became confined to river mouths they were probably completely under water. Rising of the land brought these streams again into existence, and their estuaries became populated from that of the Kennebec. Indeed, if the coast of Maine has suffered recent subsidence (see Johnson, 1925, p. ix), it is conceivable that when the land was higher than at present, estuarine conditions extended farther down the Kennebec than to-day, and the estuaries of these two creeks were confluent with that of the Kennebec.

From the Kennebec River to Penobscot Bay there is a series of long inlets, some of which have estuaries at their heads. The Sheepscot River is salt for eight miles above Wiscasset, but at Alna estuarine conditions prevail, and here grows an estuarine flora which was probably derived at some time from the Kennebec River. Although the Sheepscot is nearly a mile wide at Wiscasset, it is a small river



at the estuary, barely knee-deep at low tide. Ten miles east of Wiscasset is the Damariscotta River, which is not a true river, but a salt inlet twenty miles long, and from one-half to two miles wide. At its head a brook drains from Damariscotta Lake, fifty feet above sea level, but the influx of fresh water would not be sufficient to produce an estuary were it not for the fact that the head of the bay is cut off by a railroad embankment, which permits only a small amount of salt water to enter. Hence we find here what may be termed an artificial estuary. According to C. A. E. Long (1921, p. 199), *Ruppia maritima*, var. *subcapitata* (Fernald and Wiegand, 1914, p. 126), and *Typha angustifolia* grow here. The *Ruppia* is unknown elsewhere in Maine except on the Sheepscot River at Wiscasset (where it grows with *Fucus* and other salt-water plants), and the *Typha* is rare east of Portland. But I have seen the former plant in the salt part of the head of the Damariscotta River, while the latter may have been introduced by the trains which run through the extensive *Typha* marshes of eastern Massachusetts. Hence the Damariscotta River cannot lay claim to a true estuary. The Waldoboro River, at Waldoboro, is too small to have an estuary. The St. George River, however, is larger, and on it are found *Lophotocarpus*, *Limosella*, and *Juncus acuminatus*, which in Maine east of Portland is an estuarine species. The St. George is salt at Thomaston, and the estuary is five miles up the river at Warren.

The last large estuary in Maine is that of the Penobscot, on which have been found *Bidens hyperborea*, *Samolus*, *Eriocaulon Parkeri*, *Lophotocarpus*, and *Juncus acuminatus*, as well as *Cyperus rivularis* in its extreme eastern station. Eastward on the Union River at Ellsworth are *Bidens hyperborea* and *Limosella*, while the former plant is also found on estuaries at Cherryfield, Harrington, and Columbia Falls. I have searched the tidal shores at the last-named localities for other estuarine plants, but without success, except for the discovery of *Juncus acuminatus* at its eastern limit in the United States, on the estuary of the Cherryfield River. From here to the New Brunswick border there are several rivers—the Machias, the Cobscook, Denneys, the Pembroke, and the St. Croix—all of which are, as far as I have been able to ascertain from several expeditions along this coast, devoid of estuarine plants.

### ESTUARINE CONDITIONS ABOUT THE BAY OF FUNDY.

With the exception of the St. John and its near neighbor the Kennebecasis, the rivers entering the Bay of Fundy are completely

lacking in estuarine plants. This, in my opinion, is due to two factors.

1. The water of the Bay, in constant motion, holds in suspension a great volume of silt, derived from red sandstone and shale, so that the appearance of a great red sea is presented. (See Johnson, 1925, p. 572–574.) The Isthmus of Chignecto was formed by the water spreading over the marshes and dropping its load of suspended matter; this isthmus is therefore a delta, not of a river, but of the sea (Chalmers 1895, p. 20; Ganong, 1903, p. 167). To-day, the enormous tides—50 feet at the head of the Bay (U. S. Coast and Geodetic Survey, 1923, p. 345)—sweep the water up the mouths of the rivers, where it loses velocity and drops its burden of silt along the river shores. During the building of a bridge in this region, several steel cylinders or caissons were left anchored to rocks and exposed to the waves; in 122 days there was accumulated within each cylinder 30 inches of fine mud and sand (Murphy, 1886, p. 50–51). As if this great deposition of silt were not enough to discourage the growth of plants, the waves then tear away these clay banks, producing unstable conditions which no estuarine species could endure. On the tidal shores of the North River and the Salmon River at Truro, Nova Scotia, where this process is easily observed, I found only a few depauperate specimens of *Solidago sempervirens* and a maritime species of *Polygonum*, while a healthy stand of *Scirpus campestris*, var. *paludosus*, had its rootstocks buried a foot deep in heavy mud. From the locality where these plants grew, to the head of tide, the shores were barren of vegetation.

2. The tides of the Bay of Fundy are too great to produce an estuary, since the flood of salt water becomes so large in comparison with that of the river that all the river mouth is often drowned by it. From Truro to Parrsboro, on Minas Basin, and on the Petitcodiac River in New Brunswick, I found consistently that as far as the tide goes up the rivers, the salt water goes also. Hence, no estuaries are produced.

On the St. John and the Kennebecasis Rivers, however, conditions are different. These two streams flow into a great salt tidal bay, at the mouth of which are the famous Reversible Falls, which check the influx of the salt water just enough so that the tide is not very great in the bay, and ideal estuarine conditions are produced on the two rivers. But the number of plants which are apparently confined, in this region, to estuaries, is small: there may be listed only *Echinochloa muricata*, *Zizania aquatica*, var. *angustifolia*, *Cyperus dentatus*, *Scirpus Torreyi*, *S. fluviatilis*, *Elatine americana*, and *Bidens frondosa*, var. *anomala*. With the possible exception of the *Elatine*, none of these are necessarily identified with the fresh estuarine sea which accounts for the ranges of such plants as *Lophotocarpus calycinus* var. *spongiosus*, *Tillaea aquatica*, and *Bidens hyperborea*. In other words, the estuarine flora of the St. John and the Kennebecasis Rivers consists of plants which occur there in estuarine outpost stations.



The Reversible Falls are caused by a ledge which to some extent inhibits the effect of the tide. It is probable that at a period when the land stood higher than it does now, this ledge entirely cut off the tide from the region of the present salt bay and estuaries, making a fresh-water lake—possibly the "Lake Acadia" of Chalmers (1902, p. 11). Estuarine plants, if they were present, did not survive this destruction of their tidal habitat, with the exception of *Elatine*, which shows some ability to continue growth in a region which has recently lost its estuarine character (see page 100).

Subsidence of the New Brunswick coast[1] brought the ledges again below high-tide level, and restored the estuaries of the St. John and the Kennebecasis. As the climate grew colder, *Zizania*, *Scirpus fluviatilis*, etc., retreated from the region except where favored by the warmth of the estuaries.

Between the St. John and the St. Croix Rivers tidal conditions are not as extreme as in the rest of the Bay of Fundy, but the rivers of this part of the coast enter the sea by falls (Ganong, 1898) and estuaries are not produced.

## ESTUARINE CONDITIONS ON THE ATLANTIC COAST OF NOVA SCOTIA.

A tidal sea, fresh at its margin, once resulted where extensive drainage basins and the melting of an ice sheet produced enormous quantities of fresh water, and the advent of the ocean was perhaps somewhat checked by the now sunken edge of the continental shelf.

[1] That the coast of New Brunswick is now sinking is the opinion of several observers (Monro, 1886; Chalmers, 1895; Trueman, 1889; Ganong, 1901, 1908, 1913). Professor D. W. Johnson, in his magnificent treatment of almost exactly the same area as that considered in this paper, says (1925, p. ix–x): "It should be understood that the evidences discovered along the New England-Acadian shoreline . . . . conduct one to the same conclusions regarding the reality of a *geologically recent subsidence*, and the absence of appreciable *subsidence in historic time*." Goldthwait (1914, p. 46) expresses much the same opinion.

Along the shores of this sea estuarine plants migrated. This supposition would indicate that we should not find estuarine plants on the outer coast of Nova Scotia, which was a long way from the freshening streams. My attempts to check this theory by field observations in August, 1924, were interfered with by the poor quality of the roads between Port Mulgrave and Halifax, which were rendered almost impassable by a severe storm, but I was able to reach the Guysborough and the Country Harbor Rivers, in the northern part of the province. Guysborough Harbor is a narrow gut of salt water some five miles long; at its head the Guysborough River enters, but so steeply that no estuary is produced. On the Country Harbor River, however, there are typical estuarine conditions, but no estuarine plants. There are several plants which are estuarine in parts of their ranges, which occur in Nova Scotia on nonestuarine habitats, in all probability having reached the region as immigrants over the continental shelf, but the estuaries of the Atlantic coast of Nova Scotia, with one exception noted below, are devoid, as far as is known, of estuarine plants having affinities with the other estuarine plants discussed in this paper.

There is a river near the extreme southwestern tip of Nova Scotia which has an estuary with three estuarine plants; this is the Tusket, at whose mouth grow *Lilaeopsis lineata* in its sole station in Canada (Fernald, 1921–22, p. 110), as well as *Samolus floribundus* and *Limosella subulata*, which are present in brackish places elsewhere in the province. It is notable that these are species which are common in brackish water farther south; this may indicate that the water along the inner coast of the continental shelf was once of proper salinity to permit the growth of these plants, although it was always too brackish to allow the spread of such fresh-water estuarine species as *Elatine americana* and *Bidens hyperborea*.

## ESTUARINE CONDITIONS IN NORTHEASTERN NEW BRUNSWICK AND NORTHUMBERLAND STRAIT.

On the rivers entering the Gulf of St. Lawrence from New Brunswick, *Bidens hyperborea* is abundant. It occurs not only on the large estuaries of the Restigouche and the Miramichi, but on such smaller streams as Eel River, Benjamin River, Jacquet River, and Tetagouche River, entering Chaleur Bay. *Lophotocarpus* has not been found north of the Miramichi River, but is common on rivers from there to the Nova Scotia boundary. On this group, which



includes the Kouchibouguac (of Kent County), the Kouchibouguacis, the Richibucto, the Buctouche, and the Shediac, the *Bidens*, *Lophotocarpus*, and *Limosella* are almost always present, while *Samolus* is not rare.

East of Buctouche *Lophotocarpus* is not found, and river-mouth botanizing becomes less productive. The Cocagne River has been dammed, the Shediac River has three estuarine plants (*Bidens*, *Limosella*, and *Samolus*), while the Sadouc, the Abougoggin, the Kouchibouguac (there are two rivers of this name in the province), the Tedish, the Gaspereau, and the Tidnish Rivers seem to lack estuarine floras. In northwestern Nova Scotia, *Limosella* is found on the Shinimikas River, and *Bidens hyperborea*, var. *colpophila*, on the River Philip, near Pugwash. East of here there are apparently no estuarine plants.

The isthmus between Cumberland Basin and Baie Verte—i. e., northern Cumberland County, Nova Scotia, and southeastern Westmorland County, New Brunswick—is a low rolling country made up of land deposited, according to Ganong (1903, p. 167), by the sea. East of this the mountains rise. It is worthy of notice that the eastern limit of the occurrence of estuarine plants (River Philip) coincides with the eastern limit of this low land. It becomes evident that the communication of the plants between the Gulf of St. Lawrence and the Bay of Fundy was over this path when Chignecto was under the sea, and that they did not spread far eastward from this passage. It is possible that to the eastward the water was too salt, both because of the proximity of the ocean, and because of the smaller supply of fresh water from the then island of Nova Scotia. Northwestward, conditions were favorable to these plants, and it was in this direction that they traveled, reaching the Gaspé Peninsula and the St. Lawrence River.

Examination of the map (Pl. 8) will show the low land of the Isthmus of Chignecto, across which the water once flowed and the plants migrated. Although there are several rivers entering the Gulf of St. Lawrence from this low land (the Sadouc to the Tidnish), not one of them has estuarine plants at its mouth, although the Shediac, on the western boundary of this region, and the Shinimikas, on the eastern, are more favored. The reason for this is that at the time when estuarine plants were distributed, these rivers which now lack them were not in existence, for the land through which they now flow was then under the waves. By the time this land was

built, the water had become salt and the estuarine plants were isolated on the rivers to the east and west of this region.

The range of tide at Pugwash is four feet, and gradually decreases to a little over two feet at the Gut of Canso (U. S. Coast and Geodetic Survey, 1923, p. 344). Estuaries are produced on many of the rivers, but these are usually barren. The West River and Middle River near Pictou, and the East River at New Glasgow, are conspicuously so. On a few estuaries, especially that of the Wallace River, about eight miles east of Pugwash, saline and fresh-water types grow together. *Spartina alterniflora* has as neighbors *Scirpus rubrotinctus* and a cespitose species of *Eleocharis*. I was not able to make salinity tests here. East of Pictou the tide is so weak that there are practically no estuarine conditions produced.

In August, 1924, I collected *Samolus floribundus* on the estuary of the Shediac River, then traveled eastward for over 130 miles without seeing this species on any of the thirteen rivers which I botanized. Then, on the Antigonish River, in the extreme northeastern part of the mainland of Nova Scotia, I found it again. Here the tide is less than two feet, and estuarine conditions are almost lacking. Was *Samolus* on the Antigonish River as an isolated estuarine relic, or had it come with the Coastal Plain migration into Nova Scotia over the raised continental shelf? It is found, not on an estuary, in northeastern Prince Edward Island and in both estuarine and non-estuarine habitats in southwestern Nova Scotia. A large number of plants on the shores of the Antigonish River were growing where submerged twice daily, but an equal number of individuals grew in an open field beyond the influence of the tide. Was *Samolus* here an estuarine plant which had wandered from the estuary into the meadow, or was it a meadow type which had strayed to the estuary? I could not find this species on the river shores above the head of tide, nor did I see it elsewhere in that part of Nova Scotia.

## SUMMARY.

When a river flows into a tidal sea, an estuary is often produced. This is due to the fact that the influence of the tide may extend farther up the river than does the salt water; the region where the shores of the river are thus inundated twice a day by fresh water is termed an *estuary*. The shores nearer the ocean are naturally covered by semisaline water, and below this by nearly pure salt water.



The effect of different salinities upon the vegetation has been studied on the estuary of the Kennebec River, in southern Maine. Where covered semidiurnally by fresh water, *Sagittaria latifolia, S. graminea, Sium suave, Pontederia cordata, Polygonum sagittatum, Potamogeton epihydrus*, and other common aquatics and subaquatics are found, as well as the rarer *Bidens hyperborea*, varieties *cathancensis* and *colpophila, B. Eatoni*, varieties *kennebecensis, interstes*, and *mutabilis, Scirpus Smithii*, var. *levisetus*, etc.; where the semisaline water flows over the shores, *Lophotocarpus calycinus*, var. *spongiosus*, and *Lilaeopsis lineata* are found; and in the salt water are *Spartina alterniflora* and *Scirpus nanus*. Since the fresh water floats on the surface of the salt water, the fresh-water species may grow at the high-tide level, where reached only by the surface water, while *Spartina* is at the low-tide level, where covered periodically by the salt water, and *Lophotocarpus* is on the intermediate levels, where it is bathed at high tide by semisaline water. Going up the river from such a locality, one finds the water becoming too fresh for the *Spartina; Lophotocarpus* is confined to the lowest zone, while the fresh-water types take possession of more ground. Finally, where the water is practically or entirely fresh, the fresh-water plants occupy all levels. Conversely, as one goes downstream towards the ocean, the salt water reaches increasingly high levels, *Lophotocarpus* is confined to the high-tide level, and finally, when the water becomes entirely salt, this plant disappears. Chemical tests of the water at many points on the Kennebec River show that it actually is the degree of salinity which thus controls the altitudinal distribution of the plants.

The temperature of the water of the estuary of the Kennebec River proves to be warmer than that of the open ocean in this region, and also warmer than that of the nonestuarine tributaries of the Kennebec. This is due to the fact that the mud-flats become heated by the sun at low tide, and impart their warmth to the rising water flowing over them at flood tide.

The plants which are important in the floras of estuaries fall into four groups, as outlined below:

1. Plants which throughout the greater part of their ranges are not estuarine, but have, to the north or northeast of this continuous range, one or more stations on estuaries, where they appear to be favored by the warm water of the tidal shores.

2. Plants which are almost or entirely confined to the estuaries from northern Virginia to that of the St. Lawrence River. These seem to be relics from a period when, owing to the enormous quantities of fresh water poured into the sea from the melting of the last ice sheet, the water was rendered fresh, but still remained tidal, along the shores of this part of the Atlantic Ocean.

3. Relics from the now submerged continental shelf. These species are of European affinity, and appear to have persisted on the unglaciated edge of the continental shelf, and later to have migrated on estuaries. They are also sometimes found in nonestuarine habitats, in company with other species of somewhat similar history.

4. Plants modified by semidiurnal submergence in fresh water, so as to change their entire aspect or to lose apparently fundamental traits.

The vegetation of particular estuaries may often be linked with what is known of their geological histories. Estuarine plants are absent from: (1) the outer coast of Nova Scotia, for Nova Scotia was too far out to sea to have the waters along its shores freshened; (2) certain rivers of the Isthmus of Chignecto, which was so recently submerged that the rivers came into existence too late to receive estuarine plants; (3) the head of the Bay of Fundy, for here the great tides render conditions unfavorable for their growth; and (4) to a great extent from the St. John River, New Brunswick, for its present estuary was at one time part of a nontidal lake, when the land stood higher than at present and ledges cut off the influence of the tide (perhaps the "Lake Acadia" of Chalmers). The estuary of the Kennebec River, Maine, has a very rich flora, since it is confluent with that of the Androscoggin River; these estuaries were once separated by salt water, and on them independent floras arose, later to mingle when uplifting of the land brought these estuaries together.

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# INDEX.[1]



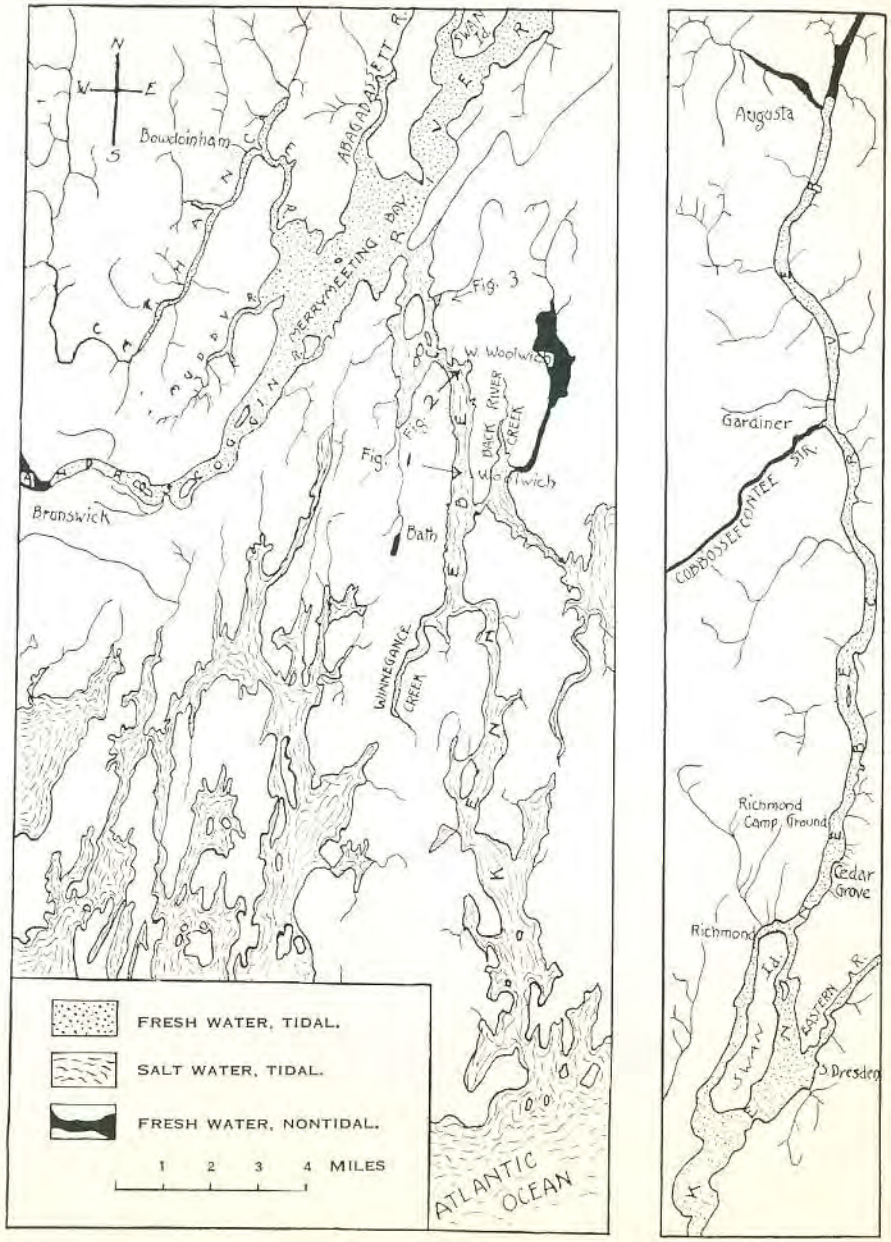
[1] Page numbers in italics indicate major references.

## EXPLANATION OF PLATES.

PLATE 6.

Map of Merrymeeting Bay, Maine, and neighboring estuaries. The right-hand section represents a northward extension of the left-hand section. "Fig. 1," "Fig. 2," and "Fig. 3," inserted on this plate in the vicinity of Woolwich and West Woolwich, show the location of the detailed maps of Plate 7.





## PLATE 7.

FIG. 1.—Tidal flats of the Kennebec River, Maine.
1. *Lophotocarpus calycinus*, var. *spongiosus*.
2. *Bidens Eatoni*, var. *interstes*.
3. *Scirpus nanus*.
4. *Spartina alterniflora*.
5. *Ranunculus Cymbalaria*.
6. *Sium suave* and *Sparganium eurycarpum*.

Circles: *Scirpus acutus*.
Stippling: *Zizania aquatica*.
Arrow indicates the direction of the photograph, Plate 14, figure 1.

FIG. 2.—Tidal flats of the Kennebec River, Maine.
1. *Lophotocarpus calycinus*, var. *spongiosus*.
2. *Scirpus americanus*.
3. *Scirpus acutus*.
4. *Spartina alterniflora*.
5. *Typha augustifolia*.

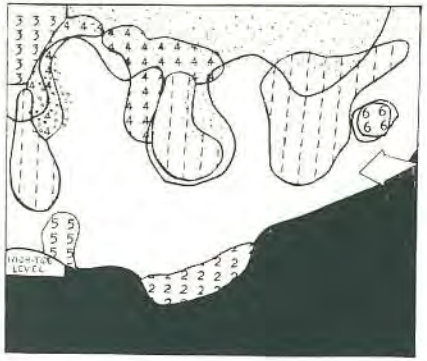
Arrow indicates the direction of the photograph, Plate 14, figure 2.

FIG. 3.—Tidal flats of the Kennebec River, Maine.
1. *Lophotocarpus calycinus* var. *spongiosus*.
2. *Lilaeopsis lineata*.
3. *Sagittaria latifolia*.
4. *Spartina alterniflora*.
5. *Myriophyllum* sp.
6. Various species; see text, pages 82–83.

Circles: *Scirpus acutus*.
Stippling: *Zizania aquatica*.
Arrow indicates the direction of the photograph, Plate 14, figure 3.

(These maps were made in the field, without surveying instruments. The outlines and scale are therefore only approximate.)



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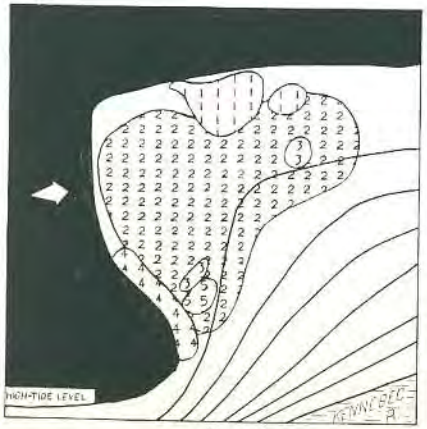


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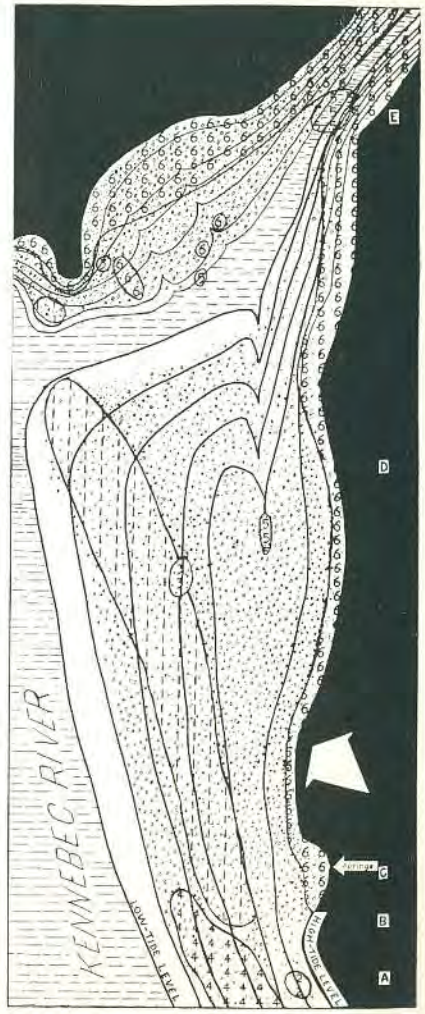


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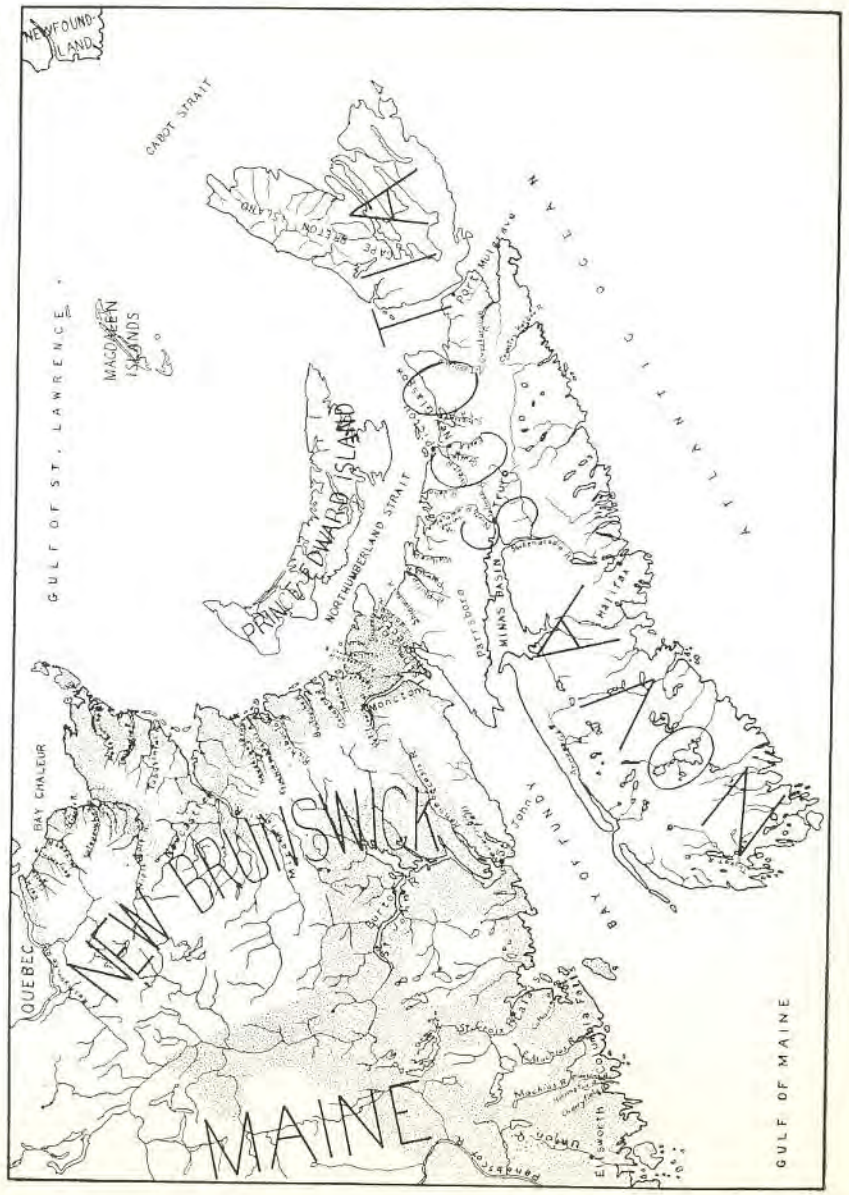
PLATE 8.

Map of New Brunswick, Nova Scotia, Prince Edward Island, the Magdalen Islands, and parts of Newfoundland, Quebec, and Maine. All the rivers of the region which are mentioned in this paper are shown. Light stippling indicates land submerged in early postglacial time (after De Geer, 1892); heavy stippling indicates the land about the Isthmus of Chignecto which is less than 20 feet in elevation (after Physical Map of the Dominion of Canada, Dept. of the Interior, Canada, 1915).





## PLATE 9.

FIG. 1.—*Sagittaria heterophylla* Pursh; eastern part of the range. Dots indicate nonestuarine stations; crosses, estuarine. Determined from the following sources: Gray Herbarium; herbarium of the New England Botanical Club; U. S. National Herbarium; herbarium of the Peabody Academy of Sciences; herbarium of Mr. Walter Deane; Stone, 1911, p. 172; House, 1924, p. 63; Harger, 1900, p. 126; Driggs, 1902, p. 39; Graves, 1901, p. 64; Knowlton *et al.*, 1910a, p. 4; Blake, 1913, p. 159; Hoffman, 1922, p. 208; Macoun, 1883–1902, p. 78–79; Grier, 1925, p. 388.

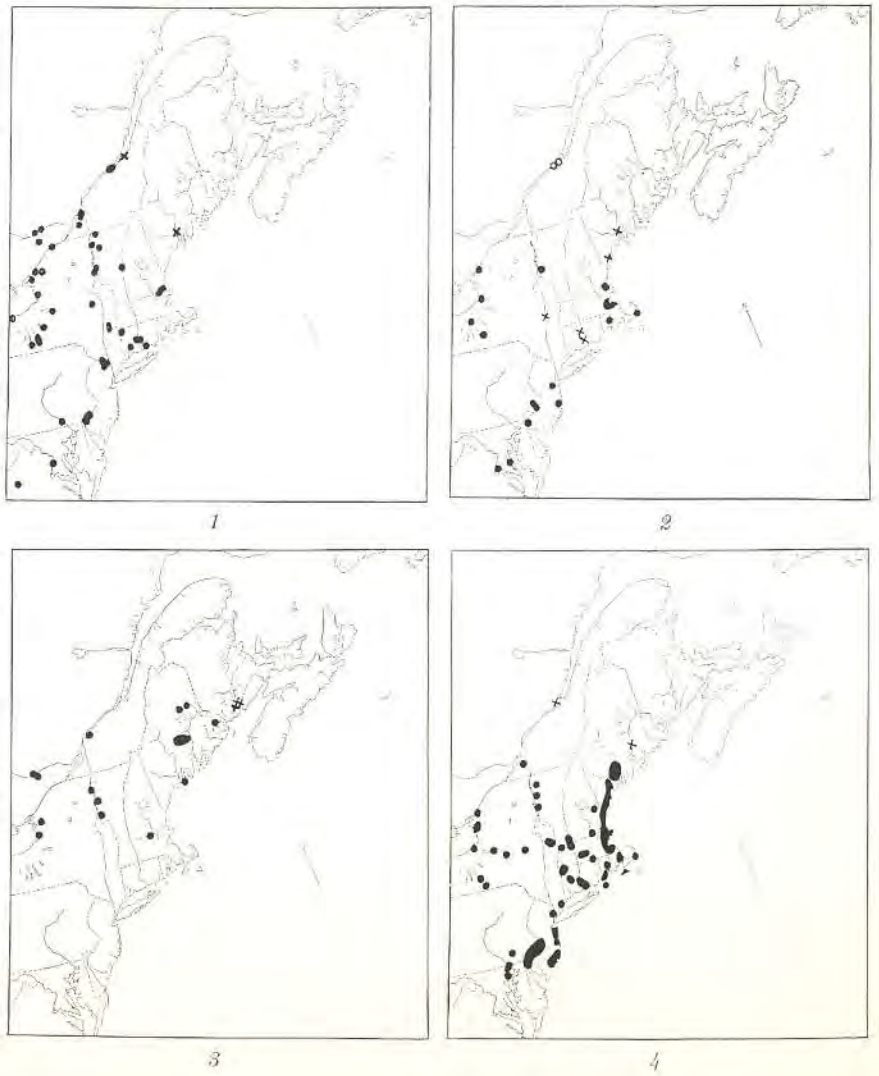
FIG. 2.—*Zizania aquatica* L.; northeastern part of the range. Dots indicate nonestuarine stations; crosses, estuarine. Determined from the following sources: Gray Herbarium; herbarium of the New England Botanical Club; U. S. National Herbarium; herbarium of Mr. Walter Deane; herbarium of the Peabody Academy of Sciences; Knowlton, Blake, and Deane, 1913, p. 123, where listed as *Z. aquatica* and *Z. palustris*.

*Z. aquatica*, var. *brevis* Fassett. Stations indicated by circles. Determined from collections in the Gray Herbarium.

FIG. 3.—*Zizania aquatica*, var. *angustifolia* Hitchc.; eastern part of the range. Dots indicate nonestuarine stations; crosses, estuarine. Determined from the following sources: Gray Herbarium; herbarium of the New England Botanical Club; herbarium of Wellesley College; herbarium of the University of Wisconsin; Harvey, 1903, p. 48, as *Zizania* sp.

FIG. 4.—*Cyperus rivularis* Kunth; eastern part of the range. Dots indicate nonestuarine stations; crosses, estuarine. Determined from the following sources: Gray Herbarium; herbarium of the New England Botanical Club; House, 1924, p. 131; Stone, 1911, p. 250; Hoffmann, 1922, p. 232.





## PLATE 10.

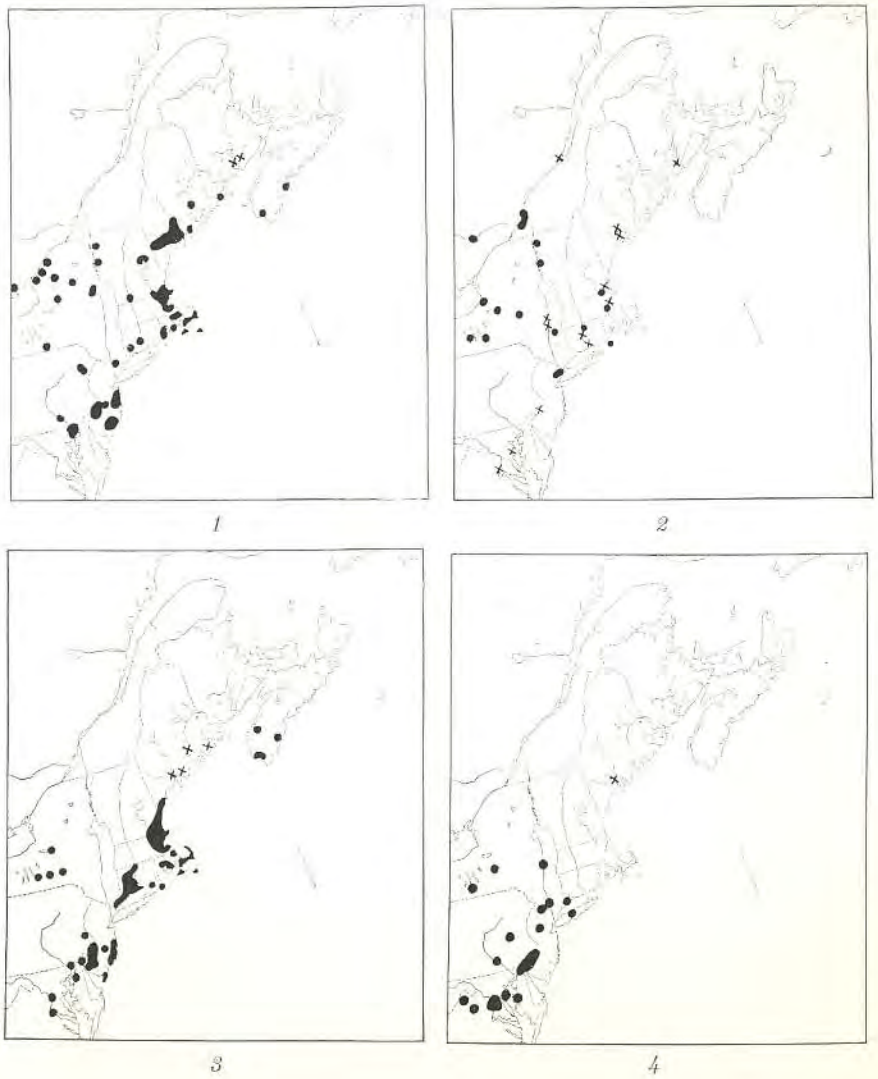
Fig. 1.—*Cyperus dentatus* Torr. Dots indicate nonestuarine stations; crosses, estuarine. Range determined from the following sources: Gray Herbarium; herbarium of the New England Botanical Club; Stone, 1911, p. 251–252; House, 1924, p. 133; Brainerd *et al.*, 1900, p. 22; Fernald, 1922, p. 162.

Fig. 2.—*Scirpus fluviatilis* (Torr.) Gray; eastern part of the range. Dots indicate nonestuarine stations; crosses, estuarine. Determined from the following sources: Gray Herbarium; herbarium of the Peabody Academy of Sciences; U. S. National Herbarium; herbarium of Mr. Walter Deane; House, 1924, p. 148; Stone, 1911, p. 271; Knowlton *et al.*, 1911, p. 84.

Fig. 3.—*Juncus acuminatus* Michx.; northeastern part of the range. Dots indicate nonestuarine stations; crosses, estuarine. Determined from the following sources: Gray Herbarium; herbarium of the New England Botanical Club; herbarium of Mr. Walter Deane; Stone, 1911, p. 336; Fernald, 1921–22, p. 242; Knowlton *et al.*, 1910b, p. 95; Bartlett, 1909, p. 230; C. A. E. Long, 1922, p. 182; Deane, 1915, p. 214; Grier, 1925, p. 395.

Fig. 4.—*Nymphozanthus advena* (Ait.) Fernald; northeastern part of the range. Dots indicate nonestuarine stations; the cross, estuarine. Determined from the following sources: Gray Herbarium; herbarium of the New England Botanical Club; Miller and Standley, 1912, p. 87; House, 1924, p. 329; Harger *et al.*, 1917, p. 130.





## PLATE 11.

FIG. 1.—*Samolus floribundus* HBK.; northeastern part of the range. Dots indicate nonestuarine stations; crosses, estuarine. Determined from the following sources; Gray Herbarium; herbarium of the New England Botanical Club; U. S. National Herbarium; herbarium of Brown University; herbarium of Mr. Walter Deane; Macoun, 1883–1902, p. 315–316; Stone, 1911, p. 631; Brainerd *et al.*, 1900 p. 69; Fowler, 1885, p. 45; Fernald, 1922, p. 179; Blake, 1918, p. 106; Grier, 1925, p. 423.

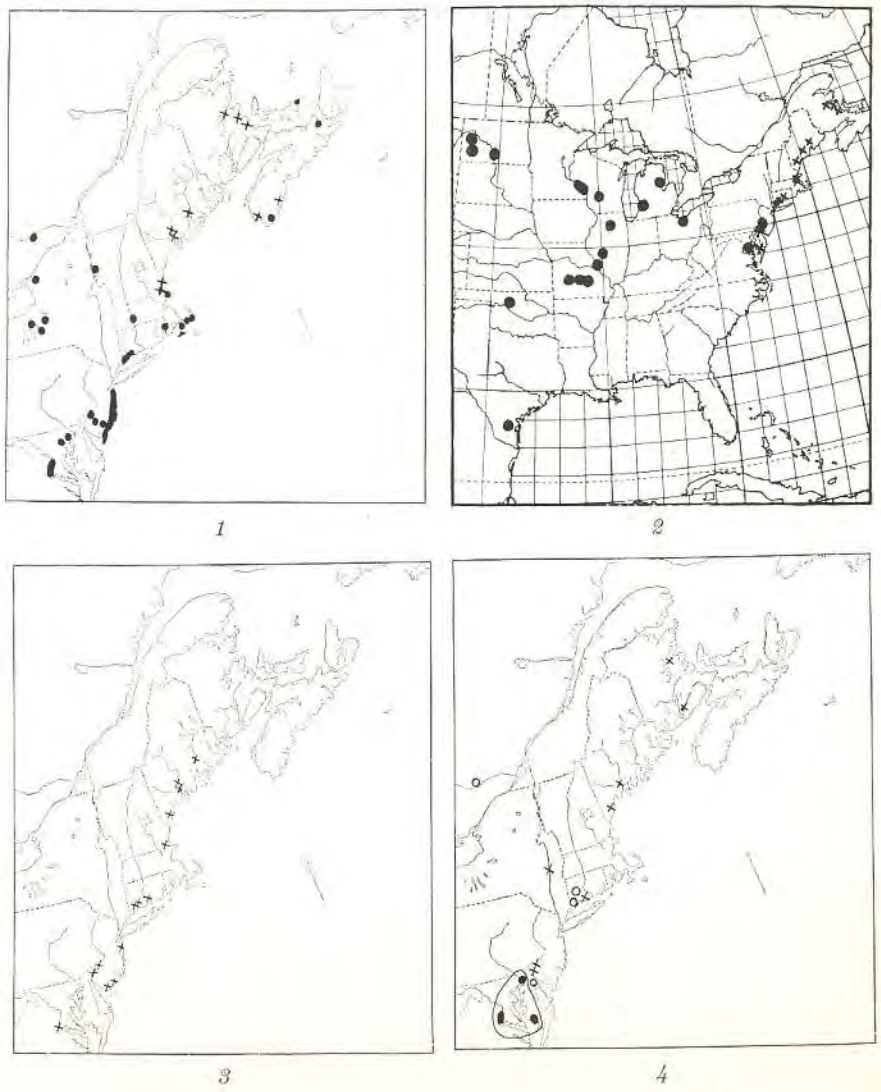
FIG. 2.—*Lophotocarpus calycinus* (Engelm.) J. G. Smith (stations indicated by dots), and *L. calycinus*, var. *spongiosus* (Engelm.) Fassett (stations indicated by crosses). Ranges determined from the following sources: Gray Herbarium; herbarium of the New England Botanical Club; herbarium of the University of Wisconsin; House, 1924, p. 62–63; Fowler, 1885, p. 67; Knowlton *et al.*, 1910a, p. 3; Woodward, 1910, p. 115; Blake, 1918, p. 102.

FIG. 3.—*Eriocaulon Parkeri* Robinson. Range determined from the following sources: Gray Herbarium; herbarium of the New England Botanical Club; U. S. National Herbarium; Harger *et al.*, 1917, p. 126.

FIG. 4.—*Elatine americana* (Pursh) Arnott. Circles indicate nonestuarine stations; crosses, estuarine. Range determined from the following sources: Gray Herbarium; Fernald, 1917a, p. 12–13; Svenson, 1925, p. 221.

*Isoëtes saccharata* Engelm. Dots within line indicate estuarine stations. Range from Shull, 1903, map.





1 2 3 4

## PLATE 12.

FIG. 1.—*Lilaeopsis lineata* (Michx.) Greene; northern part of the range, as determined from the following sources: Gray Herbarium; herbarium of the New England Botanical Club; U. S. National Herbarium; herbarium of the Peabody Academy of Sciences; herbarium of Mr. Walter Deane; Stone, 1911, p. 598–599; House, 1924, p. 535; Shreve *et al.*, p. 462; Eaton, 1900, p. 168.

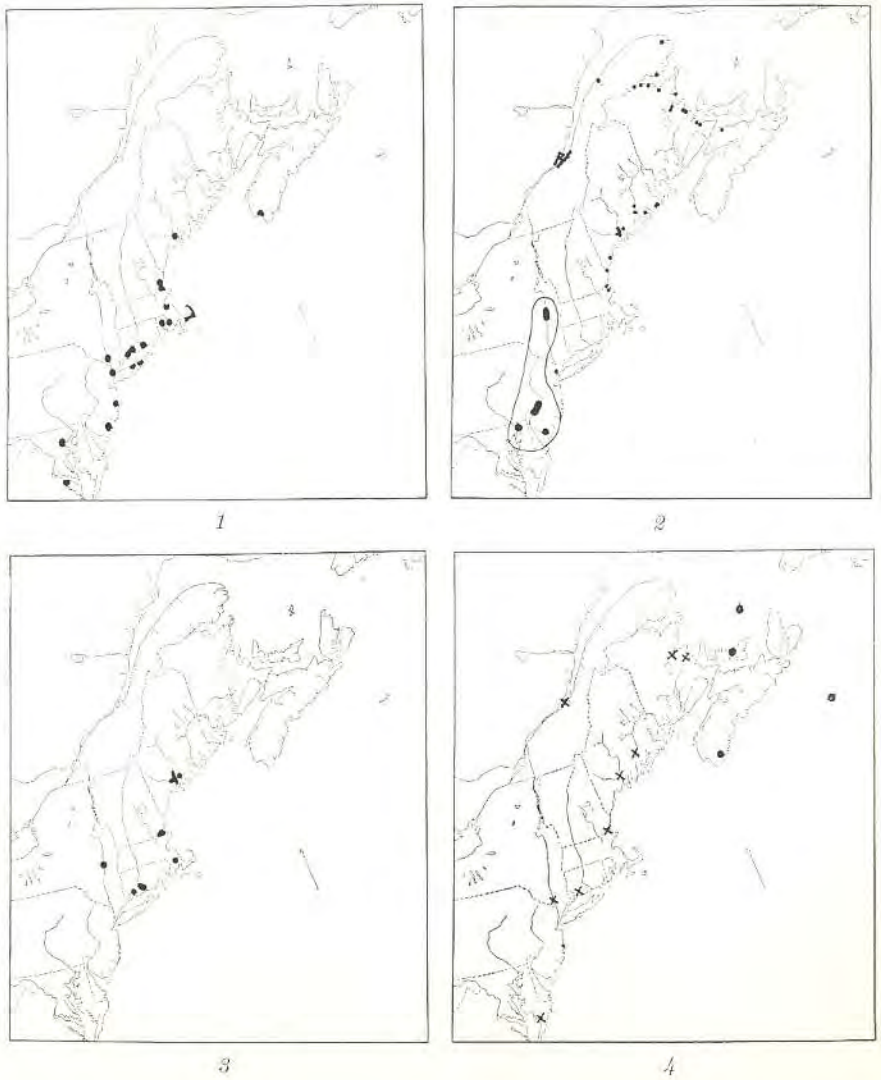
FIG. 2.—*Bidens bidentoides* (Nutt.) Britton. Stations indicated by large dots within line. Range determined from the following sources: Gray Herbarium; Stone, 1911, p. 773; Svenson, 1925, p. 221.

Varieties of *B. hyperborea* Greene, with the exception of var. *typica*. Stations indicated by small dots. Range determined from collections in the Gray Herbarium.

FIG. 3.—*Bidens Eatoni* Fernald and varieties. Range determined from collections in the Gray Herbarium.

FIG. 4.—*Tillaea aquatica* L.; northeastern part of the North American range. Dots indicate nonestuarine stations; crosses, estuarine. Determined from the following sources: Gray Herbarium; herbarium of the New England Botanical Club; House, 1924, p. 375; Fernald, 1921–22, p. 265; Blake, 1918, p. 105.





## PLATE 13.

FIG. 1.—Distribution of the genus *Lophotocarpus*, as determined from the following sources: Buchenau, 1903, p. 35–37; Smith, 1894, p. 34–35; Hooker, 1847, p. 561; Durand and Schintz, 1895, p. 487; Thiselton-Dyer, 1901–02, p. 211.

FIG. 2.—Distribution of *Tillaea aquatica* L., as determined from the following sources: Gray Herbarium; Hegi, 1922?, p. 516; Ledebour, 1844–46, p. 172; Makino, 1899, p. 120.

FIG. 3.—Distribution of the genus *Lilaeopsis*, as determined from the following sources: Gray Herbarium; Bentham, 1869, p. 374; Hooker, 1847, p. 287; Skottsberg, 1916, p. 281; Fernald, 1924, p. 569; Grier, 1925, p. 421; Weddell, 1861, p. 202.

FIG. 4.—Distribution of *Limosella aquatica* L. and *L. subulata* Ives, as determined from the following sources: Gray Herbarium; Hegi, 1922?, p. 39; Bentham, 1869, p. 503; Gmelin, 1769, p. 72–73; Matsumara, 1912, p. 561; Weddell, 1861, p. 110; Macloskie, 1904–06, p. 721; Grisebach, 1879, p. 239; Fries, 1905, p. 103; Skottsberg 1916, p. 301; Gay, 1849, p. 122; Hooker, 1885, p. 288; Turczaninow, 1856, p. 335; Muschler, 1912, p. 875; Engler, 1892, p. 378; Thiselton-Dyer, 1905–06, p. 352; Hiern, 1904, p. 357; Cheeseman, 1906, p. 489.



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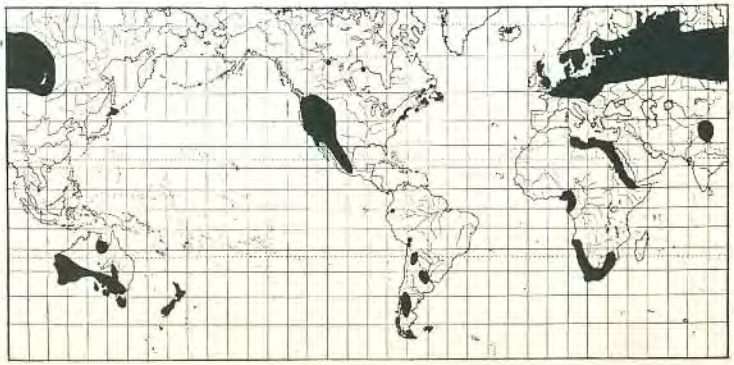

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## PLATE 14.

FIG. 1.—Tidal shores of the Kennebec River, Woolwich, Maine. Locality of Plate 7, figure 1, at low tide. In the foreground is *Lophotocarpus calycinus*, var. *spongiosus*, and behind it are *Scirpus acutus* and *Zizania aquatica*. To the left, just at high-tide level, and above the large rock, is a clump of *Bidens Eatoni*, var. *interstes*.

FIG. 2.—Tidal shores of the Kennebec River, West Woolwich, Maine. Locality of Plate 7, figure 2, at low tide. Most of the flats are covered with *Scirpus americanus*, but the comparatively bare place in the foreground is freshened by springs, and here grows *Lophotocarpus calycinus*, var. *spongiosus*. At high tide the raft at the left-hand side of the picture floats in a meter or more of water.

FIG. 3.—Tidal shores of the Kennebec River, West Woolwich, Maine. Locality of Plate 7, figure 3, looking up the river, at low tide. The conspicuous part of the vegetation of the flats is made up of *Scirpus acutus* and *Zizania aquatica*, which are nearly submerged at high tide. Some spots appear bare; here the grasses and sedges are prostrated by the action either of the wind or of the rising water.

(Photographs by Miss Katherine H. Knight.)



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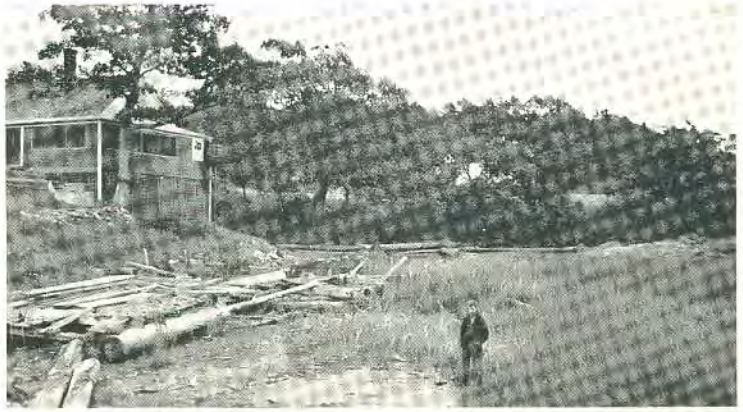

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## PLATE 15.

Fig. 1.—Tidal shores of the Kennebec River, South Dresden, Maine; the tide nearly high. Here the water shows no trace of salinity. In the immediate foreground is *Scirpus fluviatilis*, growing, as it usually does on the Kennebec, in a small clump at high-tide level. To the right is a patch of *Bidens hyperborea*, var. *cathancensis*, some of which is being collected. In the middle ground the flats are covered with *Scirpus americanus*, and to the left patches of this plant may be seen nearly submerged by the rising tide.

Fig. 2.—Estuary of the Kennebec River, West Woolwich, Maine, at low tide. Here the water is somewhat saline. *Lophotocarpus* may be seen in the middle foreground, close to the lower margin of the picture. Behind and to the right of the rocks is a clump of *Scirpus acutus*, and well to the left are dwarfed specimens of *Zizania aquatica* mentioned on page 88. In the middle ground the vegetation is largely made up of *Scirpus acutus*.

Fig. 3.—Merrymeeting Bay, Bowdoinham, Maine, at low tide. Looking east from a point between the mouth of Muddy River and that of Cathance River. At high tide the water comes to the level of the trees in the left middle ground and on the point in the left background, covering the low land to a depth of five feet. Here the water is fresh.

(Photographs by Miss Katherine H. Knight.)



*1*

*2*

*3*