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EVIDENCE FOR THE HYBRID STATUS OF ASTER × BLAKEI (PORTER) HOUSE[1]

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The aster known variously as *Aster Blakei*, *A. nemoralis* var. *Blakei* and *A.* × *Blakei* is intermediate between *A. nemoralis* Ait. and *A. acuminatus* Michx. in many ways; see figures 1, 2 and 3. Intermediate plants are encountered within the general ranges of the two species mentioned but often occur where one or the other is not evident. Thus, it has often been considered to be a hybrid of the two but about equally often interpreted as a species. Evidence of the hybrid nature of these populations has been incomplete; one or the other supposed parent is usually absent and there have been few transitional specimens connecting the more median intermediate ones with *A. acuminatus* in particular. Extensive colonies of *A.* × *Blakei* are often found at the edges of bogs, the shores of ponds, and swampy borders of woods, etc., the kinds of areas that are intermediate in wetness between the boreal forest habitat of *A. acuminatus* and the open bogs of *A. nemoralis*. Colonies of the hybrid characteristically are composed of individuals of essentially similar morphological character. The plants are large and showy and vigorous and, therefore, more easily noticed than *A. nemoralis*.

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Figure 1. *Aster nemoralis* Ait.

Note the large number of narrow, closely spaced leaves and the gradation into bracts approaching the solitary flower heads. The ligules are obviously more numerous, larger and more conspicuous than those of *A. acuminatus* in Figure 2. The interconnecting rhizome on the left hand specimens should be noted.

Figure 2. *Aster acuminatus* Michx.

Note the small number of large well-spaced leaves with coarse serrations. The peduncles are bractless and the flower heads have few rather insignificant ligules. Note the extensive rhizome which seems to be still elongating.

Figure 3. *Aster* × *Blakei* (Porter) House
Note the intermediate sized moderately spaced leaves with noticeable serrations. The gradations between bracts and large numbers of reduced leaves throughout the inflorescence can be seen. Note the extensive growth of rhizomes, characteristic of the hybrid.

Because of the abundance of *Aster* × *Blakei*, the striking effect it makes and the essential similarity of the individual plants occupying extensive areas, it is tempting to classify it as a species. As one comes to understand its biological nature as a hybrid, its mode of reproduction and its habitat requirements, there remains the possibility that it is an incipient species.

The intermediate hybrid population between *Aster acuminatus* and *A. nemoralis* has had an interesting nomenclatural history. There is general agreement now that the first name to have been given to the taxon was *Aster nemoralis* var. *Blakei* by Thomas Porter in 1894, the precise date of publication being July 20. Specimens which may be considered as syntypes were cited by Porter from Gilmanton, N. H., *Blake*, 1864 and Mt. Desert Island, Me., *Rand*, 1893. Professor C. H. Peck (1894) also had given a name to the hybrid, *Aster nemoralis* var. *major* about which there has been some confusion concerning the exact date of publication. Professor Fernald (1921) employed Peck's name but quoted Dr. House to the effect that it was unlikely that the actual printing took place before July 1, 1894. It is on this basis that priority now is accorded Porter's name, var. *Blakei*. Dr. Homer House (1919) made the new combination × *Aster Blakei*, giving Porter as the author of the basionym and indicating the Collection "Five Ponds, Herkimer County", which was cited by Peck along with the publication of his var. *major*, as typical. Shinners (1943) followed House in regarding this Aster as a hybrid though pointing out that "*Aster Blakei* is most common in sections where one supposed parent, *A. acuminatus* is rare or unknown". He also gave an accurate listing of the synonomy of the hybrid. Fernald (1950) in Gray's Manual treated the taxon as *Aster Blakei* (Porter) House though he offered the statement . . . "Sometimes called a hybrid of nos. 59 *(nemoralis)* and 61 *(acuminatus)*; rarely associated with either or both, very fertile and uniform and unknown from much of their coincident areas." To typify the name *Aster* × *Blakei* (Porter) House it is necessary to select a lectotype from collections cited by Porter. These specimens are not present at the Philadelphia Academy of Science Herbarium, where Porter's collections in major part are preserved, nor are they at the Gray Herbarium or the New York State Museum at Albany, or in other well known herbaria. Until such time as they are located, I propose that the specimen cited by House, when he made the new combination *Aster × Blakei,* be considered to accurately represent the name: Five Ponds Herkimer Co. New York C. H. Peck, Aug. without number and year. (NYS) This specimen which had been cited along with the description of Peck's *Aster nemoralis* var. *major* as typical has been carefully examined and is indeed an unquestionable example of *A. × Blakei.*

Hybridity in various groups of the American asters has received comment for many years by many authors. Wiegand stated (1928) "it was not until this phenomenon was recognized to take place under natural conditions that a number of perplexing taxonomic problems in aster were clarified." Opinions have varied both as to the widespread occurrence of natural hyridization and as to its importance in regard to species validity in *Aster.* (Avers, 1953). Herbaria have been unduly loaded with specimens exhibiting extreme variability many of which could well be of hybrid origin. This would be a natural result when one considers the tendency to collect the unusual or the different, especially when collecting is done on the individual specimen basis rather than that of population sampling. Although the concept of naturally occurring hybridization was an almost essential and compelling concept for the clarification of the taxonomy of the Aster groups, little, if any real proof was presented until the work of Wetmore and Delisle in producing artificial controlled hybrids between *A. novae-angliae* and *A. ericoides* (1939) followed by Avers (1953) in the Heterophylli series. Both cases showed that controlled artificially produced F1, F2 and backcrossed hybrids were frequently identical with collected specimens of perplexing taxonomic standing. What had been a strong hypothesis now had the validity of experimental proof. The use of the hybrid index for population analyses has confirmed and delineated the occurrence of natural crossing between good species in other groups of asters and in some cases involving whole taxonomic series. (Cronquist, 1949).

Observations of collectors have indicated that *Aster Blakei* when found with one of its putative parents has been more often associated with *A. nemoralis* than with *A. acuminatus*. This could be interpreted as an indication of habitat preference of the hybrid progeny for the open, well-lighted areas occupied by *A. nemoralis* as opposed to the shady protected habitat of the other parent, *A. acuminatus*. On the other hand, this might well have a genetic compatibility basis whereby backcrossing and hence introgression may occur more readily or successfully in the direction of one parent than the other, in this case in the direction of *A. nemoralis*. This latter explanation also seems to be supported by field and herbarium data. It is a significant fact that *A.* × *Blakei* has often been regarded as a variety of *A. nemoralis* with sometimes suggestions of hybridity with *A. acuminatus* but that no collector of record has indicated that this aster might be a variety of *A. acuminatus*. The greater number of specimens in herbaria which more nearly resemble *A. nemoralis* than *A. acuminatus* is noticeable and population sampling of many colonies confirm this generalization.

On August 22, 1960, an unusual opportunity offered itself to present proof of the hybrid origin of this taxon. While the author and A. R. Hodgdon were on a trip to Outer Wood Island, one of the outlying islands of the Grand Manan archipelago in the Bay of Fundy, they came across a group of asters which was an obvious hybrid swarm between *Aster nemoralis* and *A. acuminatus*. These asters were growing in a narrow, wet, boggy meadow between white spruce and balsam fir woods and a cobble beach. The large pink flowers of *Aster nemoralis* always attract attention, but this group was especially arresting because of the intergrading forms from typical *A. nemoralis* to those approaching *A. acuminatus.* It was a rainy, foggy, windy, and altogether unpleasant day, and in some haste, specimens were gathered to fill the vasculums. The material was gathered with an eye for diversity yet, more or less, at random. It was probably a fair sampling of the population. Notes made at the end of the day back at the hotel at Castalia on Grand Manan read . . . "Interesting Asters — appears to be × series between *A. nemoralis* and *A. acuminatus* — made a representative collection."

Weatherby and Adams (1945) in their Vascular Flora of Grand Manan reported *Aster acuminatus* as "the commonest aster of the island". For *A. nemoralis* they gave various specific locations "in sphagnum" including White Head Island and Inner Wood Island but not Outer Wood Island; however, since no collections in their list are specifically ascribed to Outer Wood Island, possibly they did not collect there.

In regard to "*Aster nemoralis* var. *major* Peck (var. *Blakei* Porter)", they observe that it "occurs in moist ground at Rich Pond on Ross Island and at Deep Cove (6635) : regarded, quite plausibly, by House and Shinners as a hybrid between *A. acuminatus* and *nemoralis.*" They then agree with other observers that "if a hybrid, however, it is an exceptionally common cross, or self perpetuating", still leaving doubt as to its hybridity.

The series of asters collected on Outer Wood Island in 1960 were analyzed by the hybrid index as developed by Edgar Anderson (1936). The use of the hybrid index allows a study of populations where hybridity is suspected and furnishes an analysis that is hardly possible by any other means.

For this particular hybrid index nine characters from the key and species description in Gray's Manual of Botany, 8th Edition, plus one additional character were selected as follows:

1. Number of leaves.
2. Ratio of leaf measurements — length divided by width.

3. Distance in mm. between median internodes.
4. Degree of revoluteness of leaf margins.
5. Degree of scabrosity of leaf margins.
6. Leaf serrations.
7. Number of bracts on peduncles.
8. Number of heads in inflorescence.
9. Ligule color.
10. Zebra hairs.

Phyllary characteristics usually of importance in taxonomic descriptions of asters were omitted because they seemed of little importance as reliable characters within this group but serve rather in distinguishing this group from other American asters.

1. The number of leaves was chosen as an important character because the two presumed parental species are so different in this respect. While *Aster nemoralis* may have one hundred or more leaves, *A. acuminatus* seldom has more than twenty leaves. Accuracy of observation is possible in a numerical character such as this and allows for as many assigned values as the importance of the taxonomic character warrants. Seven values were assigned from 0 to 6 as follows: from 35 leaves to 100 or more = 0, from 34 leaves to 32 = 1, from 31 leaves to 29 = 2, from 28 leaves to 26 = 3, from 25 leaves to 23 = 4, from 22 leaves to 20 = 5, from 19 leaves or less = 6.

A specimen scoring 0 would, in respect to leaf number, be typical of *Aster nemoralis* and a specimen of score 6 would be typical of *A. acuminatus* for this character, the intermediates forming a series, hybrid for this particular character.

2. The ratio of leaf measurements was an obviously important characteristic because of the very different shapes of the leaves of these two asters, those of *Aster nemoralis* being narrow or linear lanceolate while those of *A. acuminatus* are about three times as long as broad. The measurement of leaf length divided by width gives a ratio which expresses the shape and character of the leaf which is of

greater taxonomic significance in distinguishing these two species than any single measurement and the effect of variations in edaphic conditions are at the same time largely eliminated.

Ratios of 10 to 7 were assigned the value of 0 as the leaves of *Aster nemoralis* are from ten to seven times as long as wide. Ratios less than 7 and down to 5 were given the value of 1; of less than 5 and including 4 the value of 2; of less than 4 and down to 3.33 the value of 3; while all lesser ratios were assigned the value of 4. Any specimens having this last value would have leaves not over three times as long as wide which would be typical of *A. acuminatus*. Again, this was a character of real taxonomic importance that allowed accurate observation and division into significant sections.

3. The distance between leaves is diagnostic in describing these two species. The leaves of *Aster nemoralis* are crowded being usually between one and eight millimeters apart while the leaves of *A. acuminatus* are widely spaced, being up to three centimeters apart. The median section of the stem was chosen as the site of measurement to secure truly comparable data. Values were established as follows: 1 to 8 mm. = 0, 9 to 11 mm. =1, 12 to 14 mm. = 2, 15 to 18 mm. = 3, 19 to 23 mm. = 4, 24 to 30 mm. or more = 5.

Admittedly, edaphic conditions could influence these values but it is doubtful if the greatest measurement for *Aster nemoralis* would equal the smallest for *A. acuminatus*. As these values were established for the study of populations where edaphic conditions would be considered somewhat uniform, it was felt that they had sufficient validity.

4. Revolute leaf margin is a strong and constant character of *Aster nemoralis* while flat leaf margin is an equally constant diagnostic feature of *A. acuminatus*. A cursory examination of the specimens to be indexed indicated almost every possible variation of revoluteness and it was obvious that regardless of the desirability of establishing numerous

grades for this important character it would be impossible to accurately classify the material. Hence only four values were established: unquestionable revoluteness with a value of 0 as typical of *A. nemoralis* and unquestionable flatness with a value of 3 as typical of *A. acuminatus* with two intermediate values of 1 and 2.

5. Scabrous leaf margins in *Aster nemoralis* are opposed to hairy margins in *A. acuminatus* and an examination of the material showed a continuous variation that would defy accurate separation into discreet values. Therefore, only the categories scabrous = 0, hairy = 2, and median = 1 were established.

6. The leaves of *Aster nemoralis* are entire while those of *A. acuminatus* are serrate to strongly serrate. The specimens at hand exhibited intermediate conditions but nevertheless separated into four well-marked groups; big serrations, small serrations, presence of a tip gland and not serrate, the latter having the value of 0 for *A. nemoralis* and the value 3 assigned for big serrations as typical of *A. acuminatus*. The presence of the gland having the value of 1 and small serrations 2.

7. The number of bracts on a peduncle presents somewhat of a quandary as in *Aster nemoralis* the leaves grade imperceptibly into bract-like structures, and there is no clear delineation of the peduncle. *A. acuminatus* on the other hand has distinct peduncles which have very few, to no bracts. (In *A.* × *Blakei* the inflorescence may be bracted to heavily bracted to almost foliaceous.) A scale was set counting four to many bracts as a character of *A. nemoralis* with the value of 0; three bracts with the value of 1, two bracts 2, and the presence of only one bract or none with the value of 3.

8. Although *Aster nemoralis* may have more than one head to an inflorescence, the single headed condition is very frequent and it was chosen to score it as characteristic, with the value of 0. Multiple heads almost invariably found

in *A. acuminatus* was given a score of 1. It is reasonable to suspect that this factor may be influenced by edaphic conditions. (*A.* × *Blakei* may have very great numbers of heads, to more than one hundred.)

9. Ligule color can be a fleeting thing, especially with herbarium specimens, where so much depends on collecting conditions and subsequent techniques of preservation. However, *Aster nemoralis* has colored ligules from bright, pure pink to lilac pink to rare crimson. The only specimen of *A. n.* f. *alba* Fern. examined was a seeming hybrid. The white to whitish ligules of *A. acuminatus* seldom display color even with aging and when there is a trace of pink, one may suspect introgression. Consequently, the presence of color was given the score of 0, a trace 1, and white 2. With perfect material more grades might be established.

10. The character "Zebra hairs" needs clarification (Figure 4). This is the name used for the hairs with reddish septations so abundant on the stem of *Aster acuminatus*. Under 30× magnification, the septa, which alone contain the red pigment glow like rubies giving a striated or zebra-like appearance to the hairs. Such hairs are entirely lacking on *A. nemoralis*. The occurrence of these hairs varies from abundant on *A. acuminatus* to sparse without the ruby coloring of the septa to completely absent on *A. nemoralis*. This character, while previously unused in describing *A. acuminatus*, seems useful for this hybrid index because its expression appears to be governed by additive factors.

An additional character could possibly be used in analyz-

Figure 4.

Enlarged (c.22×) photograph of stem-petiole area: *Aster acuminatus*: This specimen scored 26 on the hybrid index and would key to *A. acuminatus*. Note the dense curled and twisted hairs on the stem. This condition was rated abundant and scored the maximum of 2. Careful examination even in this black and white reproduction will reveal the striated condition that suggested the name "zebra hairs." These hairs are always found on *A. acuminatus* and are entirely absent on *A. nemoralis*.

ing this group as Torrey and Gray (1841) in describing the lower leaf surfaces of *Aster nemoralis* say "minutely dotted with resinous globules." A sampling survey of five hundred specimens ranging from *A. nemoralis* thru *A.* × *Blakei* to, and including, high scoring *A. acuminatus* shows this character with intense expression in *A. nemoralis*, somewhat lessening in *A.* × *Blakei* with a gradual decrease toward the end of the series approaching *A. acuminatus*. However, even specimens in this series with the highest scores showed, on close examination under 30× magnification some slight expression of this character. The presence of these globules which come to resemble glandular hairs when present in *A. acuminatus* bear little relationship to the presence of zebra hairs, both characters seemingly independently inherited in additive degrees.

While these resinous globules might make an additional character for the hybrid index however because of the practical difficulties of good quantitative measurement it would be hard to establish many categories. It seems in this series of specimens which all came from areas of overlapping range of the parental species the character of "resinous globules" has made complete introgression in some degree from one species into the other. An examination of the exposed lower leaf surfaces of the specimen in Figure 2, which was collected in Coos County, N. H., where no *A.* × *Blakei* has been recorded, failed to reveal any resinous dots. This should be pursued further in the examination of specimens not only beyond the range of recorded hybridity but where *A. nemoralis* itself does not occur.

During the next few years additional collections from different localities were assembled, several through the interest and courtesy of other collectors (Table 1). All specimens were scored by the hybrid index and each collection plotted on a diagram. The hybrid index ratings of selected characteristic populations is shown in Figure 5 with explanations. In addition all specimens of the three taxa *Aster nemoralis, A.* × *Blakei* and *A. acuminatus* in the herbaria of the New England Botanical Club and the Uni-

Table 1

STATION	LOCATION	TYPE OF HABITAT	COLLECTOR	DATE
Brier Island Road to North Light	Canada Nova Scotia Digby Co.	Very wet (drainage from higher elevation) rocky meadow on exposed headland	Hodgdon, A. R. & A. M. R. B. Pike R. I. Denbow	8/18/62
Peajack Road	Same as above	Abandoned road thru coniferous and mixed woods with wet sphagnous sections and open drier areas	"	8/19/62
Western Pt.	Same as above	Low central area with shrubby hummocks. Ledges on margins with coniferous woods and alders	"	8/20/62
East Wolf South West Cove	Canada New Brunswick Pennfield Parish Wolf Islands	Margin moist woods, south end barrier beach	Hodgdon, A. R. & A. M. R. B. Pike C. Saltonstall R. Burns	

STATION	LOCATION	TYPE OF HABITAT	COLLECTOR	DATE
Outer Wood Island	Canada New Brunswick Charlotte Co. Grand Manan	Narrow, wet, boggy meadow between white spruce, balsam fir woods and a cobble beach	Hodgdon, A. R. & R. B. Pike	8/22/61
Outer Wood Island	Same as above	Woods and small meadows adjoining original collection area, semi-shaded glades — depressions between ledges — with some higher and drier areas — juxtaposed habitats for both aster species and hybrids	Pike, R. B. J. B. Pike	8/21/63
Southern Head	Same as above	Peaty area above high cliffs on exposed headland — dominated by *Potentilla fruticosa*. Some alders, scattered conifers — asters in openings between	Pike, R. B. J. B. Pike	8/21/63

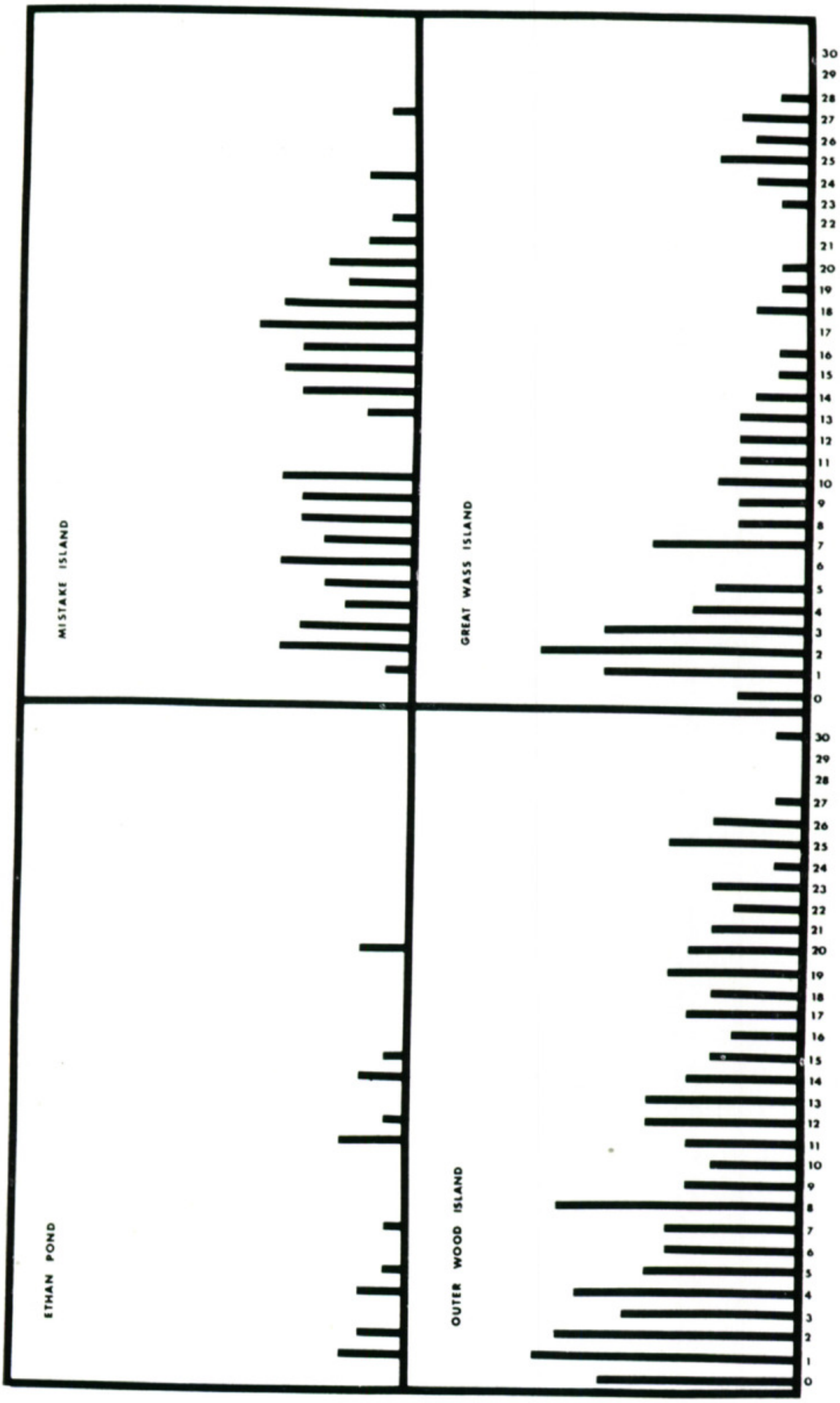
STATION	LOCATION	TYPE OF HABITAT	COLLECTOR	DATE
Mistake Island	Maine Washington Co. Jonesport	30 ft. swath kept open thru a growth of white spruce, balsam fir and alders. Moist spongy turf fully occupied with grasses, sedges and asters	Pike, R. B.	9/15/63
Mann Island	Maine Washington Co. Jonesport	Almost bare granite island with bog in central basin — a few shrubs & conifers on margins and in larger crevices of ledges	Pike, R. B.	9/15/63
Great Wass Island	Maine Washington Co. Beals	Point sparsely wooded with conifers, small marshy area between alders and beach — with suitable habitats for both species and hybrids	Hodgdon, A. R. & R. B. Pike	8/23/63
Near National Park Cabin	Maine Knox Co. Isle au Haut	Steep rocky banks of stream in spruce arbor-vitae forest	Hodgdon, A. R. & David Wise	9/12/68

STATION	LOCATION	TYPE OF HABITAT	COLLECTOR	DATE
Back Narrows	Maine Lincoln Co. Boothbay	Bog open-wet-clumps shrubs and low forest *Abies balsamea*, *Larix laricina*, *Picea rubens*, *Aster nemoralis* in wet areas, *A. acuminatus* in wooded areas, *A.* × *Blakei* in intermediate spots	Hodgdon, A. R.	8/31/62
White Lake	New Hampshire Carroll Co.	Steep sandy talus bank on shore of lake with mixed woods above and in back	Straus, C. M.	9/7/64
Chocorua Lake	Same as above	Sandy peaty area on shore of lake	Steele, F. L.	8/25/62
Ossipee Lake	New Hampshire Carroll Co. Ossipee	Lake margin with sandy beach grading into peaty area and backed by swampy woods	Hodgdon, A. R.	9/17/62
Ethan Pond	New Hampshire Grafton Co. Bethlehem	Boggy margin of lake	Steele, F. L.	8/13/62

versity of New Hampshire were scored thus giving a broad spectrum of specimens over much of the range. All hybrid index scores of 972 specimens were combined in a summation diagram (Figure 6).

A further analytical technique that often proves useful in studies of natural hybridity is the "scatter diagram" (Figure 7). It demonstrates hybridity within a population but only for two characters. However by adding supplementary symbols for other characters, linkage patterns may appear. After making scatter diagrams for many pairs of characters and for most populations studied, it was apparent that the hybrid index shows the hybrid relationship more completely.

An interesting skew toward *Aster nemoralis* (Figure 5, Outer Wood and Great Wass Island populations) becomes striking with consolidation of the scores (Figure 6). The five values at either end are typical of the parental species yet show expected intraspecific variation. Plants scoring from 8 to 19 would fit *A. Blakei* according to the description in the 8th Edition of Gray's Manual. Plants with scores from 5 to 7 and from 20 to 25 show varying degrees of introgression toward the parental species and present difficulties of classification which become obvious in examining collections in herbaria. These categories have made the classification of these asters impossible without recognizing their hybridity. The skew of the graph toward *A. nemoralis* not only represents a greater number of individuals but it should be emphasized that these are usually biologically successful as becomes evident upon an examination of the plants involved. A comparable survey of the plant material comprising the scores introgressing toward *A. acuminatus* shows not only a distinct reduction in numbers but a series of relatively poor and often strange-looking plants. Possibly the backcross to *A. acuminatus* produces biologically less successful progeny than the backcross to *A. nemoralis*. It may be that in this area the sterile forms originate that are described as *A. a.* f. *discoideus* by Kutze and *A. a.* f. *virescens*, *Victorin* and *Rous-*


MISTAKE ISLAND
GREAT WASS ISLAND
ETHAN POND
OUTER WOOD ISLAND

seau. These asters with pom-pom heads of empty chaff have been an enigma as well as a fascination to collectors. The latter is attested by the remarkable number which occur in herbaria. As the possibility of pathological origin exists, these forms were not considered in this study.

It is probably significant to note that although *Aster Blakei* has been considered as a variety of *A. nemoralis* no botanist has suggested that it might be a variety of *A. acuminatus.* This reflects the position of *A.* × *Blakei* as demonstrated in the graph of Figure 6 which shows it to have more characters of *A. nemoralis* than *A. acuminatus.* This tendency is shown in looking through folders of specimens in herbaria as one often finds *A. Blakei* classified wrongly as *A. nemoralis,* but only very rarely does one find an *A.* × *Blakei* in a folder of *A. acuminatus.*

Figure 5.

All four of the populations plotted on the above diagrams show introgression with a wide range of scores derived from the hybrid index. Both 1960 and 1963 collections totaling 158 specimens were used to construct the Outer Wood Island table since the areas of collection were adjoining and more or less continuous and only weather prevented their being collected at one time. This was the first area showing full range from *Aster nemoralis* to *A. acuminatus* with a strong middle range of *A.* × *Blakei.* No record exists of any previous observation of such a population.

The table for the Great Wass Island population is equally striking, although composed of only eighty-nine individuals. Mistake Island is a third maritime station with comparable ecological conditions and its population sample also of 89 specimens displays a practically complete range of hybrids as well as good examples of the parent species.

Ethan Pond in the White Mts. of New Hampshire at an elevation of 2,900 ft. can be regarded as a montane habitat. The population sample of 17 specimens collected here by Frederic Steele, while not as large as shown in the other tables, shows a range of specimens from good *Aster nemoralis* to *A.* × *Blakei* and a few specimens with some tendency toward *A. acuminatus.* The population at this station can be regarded as nearly typical of previous collecting sites with few if any specimens showing obvious characters of *A. acuminatus,* the absence of suitable habitat not favoring this sector of the population.

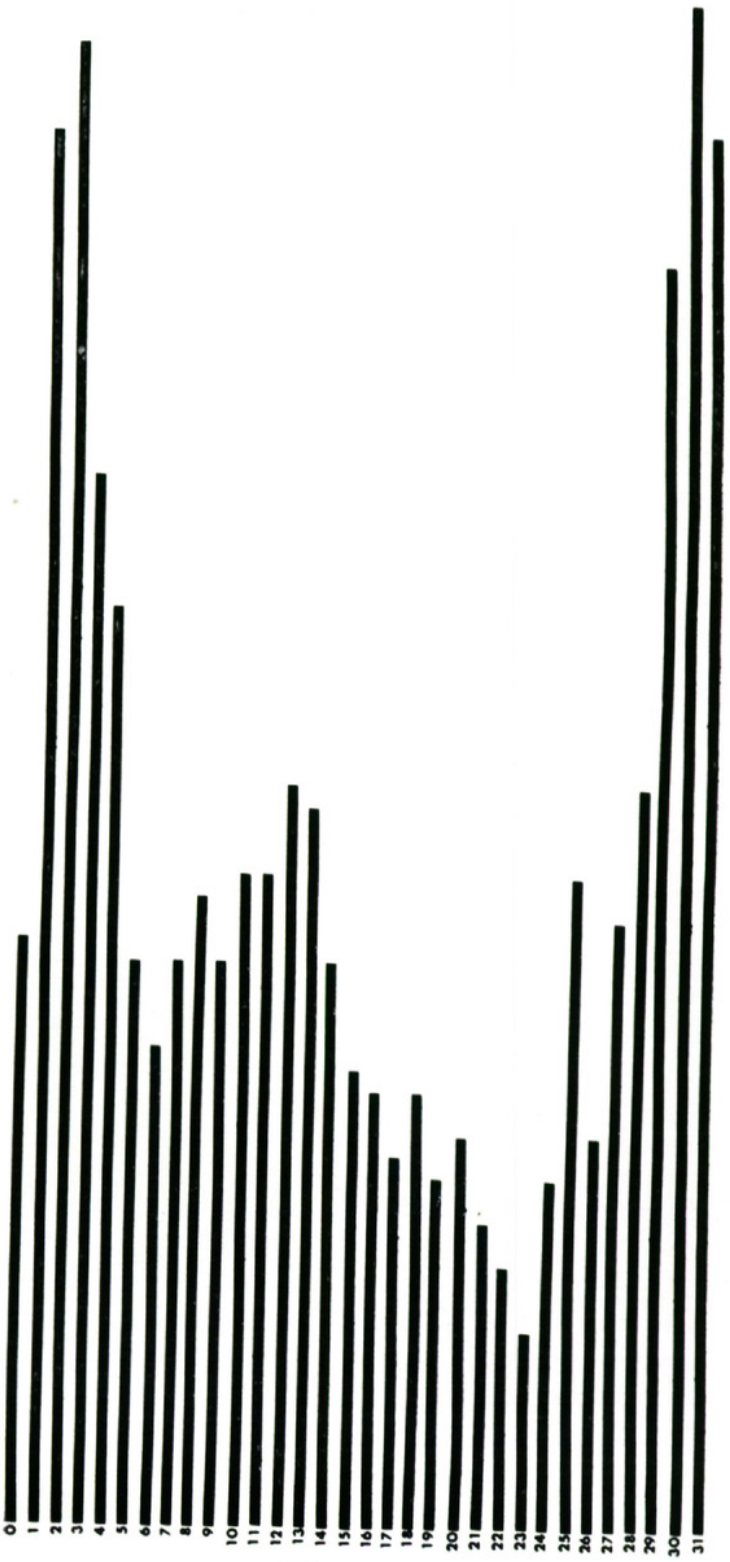


Figure 6.

Hybrid index ratings of 972 specimens of *Aster nemoralis*, *A.* × *Blakei* and *A. acuminatus* in the herbaria of the University of New Hampshire and of the New England Botanical Club at Harvard and the collections listed in Table 1. *A. nemoralis* at the left (0-4), *A.* × *Blakei* in the center (8-19), *A. acuminatus* at the right (25-31). The remaining numbers are the intergrading intermediates.

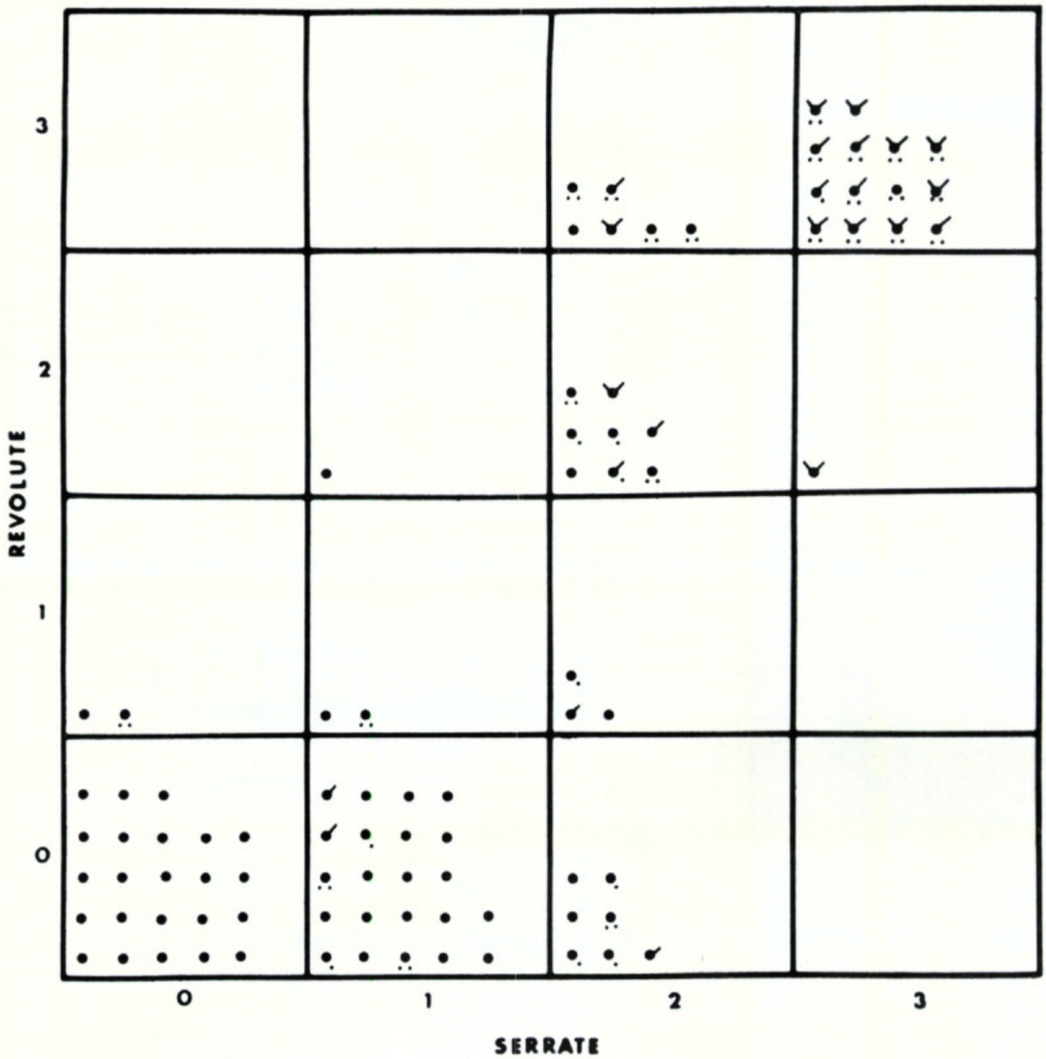


Figure 7.

Scatter diagram of Aster population from Great Wass Island plotted for two leaf characters, each of which had been assigned four values, from zero to three. Revolute leaves, with no serrations characteristic of *Aster nemoralis* (assigned value 0) are plotted in the lower left corner. Flat leaves with large serrations characteristic of *A. acuminatus* (assigned value 3) are placed in the upper right corner. The remaining plants are placed in squares according to their scoring for these two characters. Thus, this diagram shows hybridity of the intervening plants only for these two leaf characters.

The supplementary symbols indicate the distribution of two other characters, in this case median internode length and bracts on peduncle. The rabbits ears indicate increasing internode lengths and the small dots decreasing numbers of bracts on the peduncle. (See hybrid index for scores.) Similar diagrams were made for the thirteen population collections under analysis, but while they are valuable for studying pairs of characters and possible linkages they do not give a comprehensive demonstration of total introgression that is afforded by Fig. 6 which is based on all ten characters.

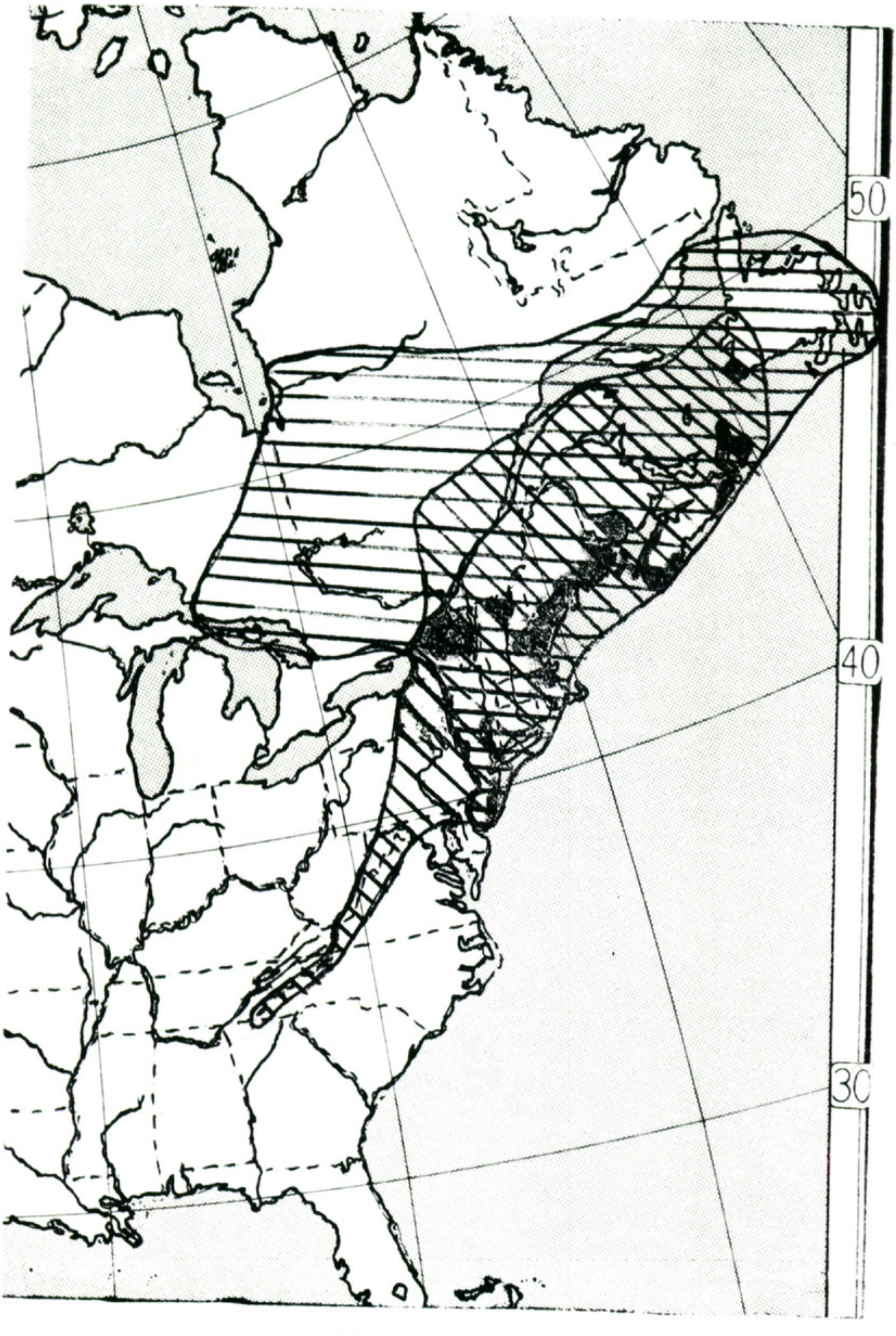


Figure 8, Map.

The geographical range of *Aster nemoralis* is indicated by horizontal lines and *A. acuminatus* by diagonal lines. Shading indicates areas from which collections of *A.* × *Blakei* have been recorded. Note that there are no records of the hybrid outside the cross-hatched section.

While both *Aster nemoralis* and *A. acuminatus* are northern and eastern asters, their ranges (Map, Figure 8) are not quite the same. *A. nemoralis* is found in most of Newfoundland, along the north shore of the Gulf of St. Lawrence including Anticosti Island, in the basins of the Rupert and East Main rivers that run into James Bay, the southern tip of Hudson's Bay, to the junction of Lakes Huron and Michigan, in northern New York state south along the coast to Cape May, New Jersey, in addition to the New England states and the Maritime Provinces.

The range of *Aster acuminatus* is northern yet does not extend as far north as *A. nemoralis.* Jennings (1953) says of it: "This northern aster which requires a cooler climate, evidently has migrated up into the mountains and northward since the melting away of the glacial ages." It barely extends into Newfoundland and along the St. Lawrence from the Saguenay River to Ottawa, north to Lac St. Jean, then south along the Appalachians to the junction of Tennessee, North Carolina and Georgia, much of New Jersey and New York as well as New England and the Maritime Provinces.

It is only within the overlapping ranges of these two species that *Aster × Blakei* has been recorded. The areas of collection have been primarily, but not exclusively, maritime or montane and are notably discontinuous. There is the strong suggestion that the conditions allowing the formation of the hybrid, *A. Blakei,* have occurred at numerous times and places and that either one or both parents have not survived subsequent ecological changes. Apparently, the only areas at the present time with the proper coincidence of habitat and meteorological conditions are the few reported stations on the Maine Coast and Bay of Fundy.

Fernald's statement (1950) regarding *Aster × Blakei,* "Sometimes called a hybrid of nos. 59 and 61, rarely associated with either or both, very fertile and uniform and unknown from much of their coincident areas" needs to be examined critically. Observation in the field as well as in herbaria shows *A.* × *Blakei* to be almost invariably associated with the parent *A. nemoralis* and careful search will often disclose evidence of *A. acuminatus* not too far away. In twelve stations observed in this study both parents and the hybrid have been found growing in close proximity. Fernald's assumption of fertility may not have had much scientific basis. What may appear to be separate plants in an area may in reality be one or more clonal groups connected by underground rhizomes*. Collections many years apart indicate these clonal groups are long lived and persistent. These same facts explain his comments on the uniformity of the plants.

As for being unknown from much of the coincident area of the parents the important fact is that it occurs only in this coincidental area. When the specialized habitats of the parents are considered the points of contact where hybridization can take place are indeed limited which would impose a discontinuity of distribution.

The transition from wet sphagnum bogs to coniferous woodland is of common occurrence in northern New England and the Maritime Provinces. The transition areas are usually dominated by ericaceous shrubs and tall sedges and grasses, then rather abruptly grade into taller thickets of *Myrica gale, Nemopanthus, Ilex verticillata, Salix* spp. and finally alders before the coniferous species dominate on higher and drier areas. The habitat of *Aster nemoralis* is the open bog, often the wettest spots where there is little

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*The distinction between stolon and rhizome is confusing at best. Fernald (1950) used both terms in describing *Aster nemoralis*. Whether he meant them synonymously is not quite clear. In his glossary he defines rhizome as, "Any prostrate or subterranean stem, usually rooting at the nodes and becoming upcurved at the apex." Stolon is defined as, "A runner or any basal branch that is inclined to root." Gray (1887) says a stolon is "a branch from above ground which reclines or becomes prostrate and strikes root . . .", while "a rhizome (Rhizoma) . . . is merely a creeping stem or branch growing beneath the surface of the soil, or partly covered by it." The latter definition from Gray is the sense in which the term rhizome will be used in this paper.

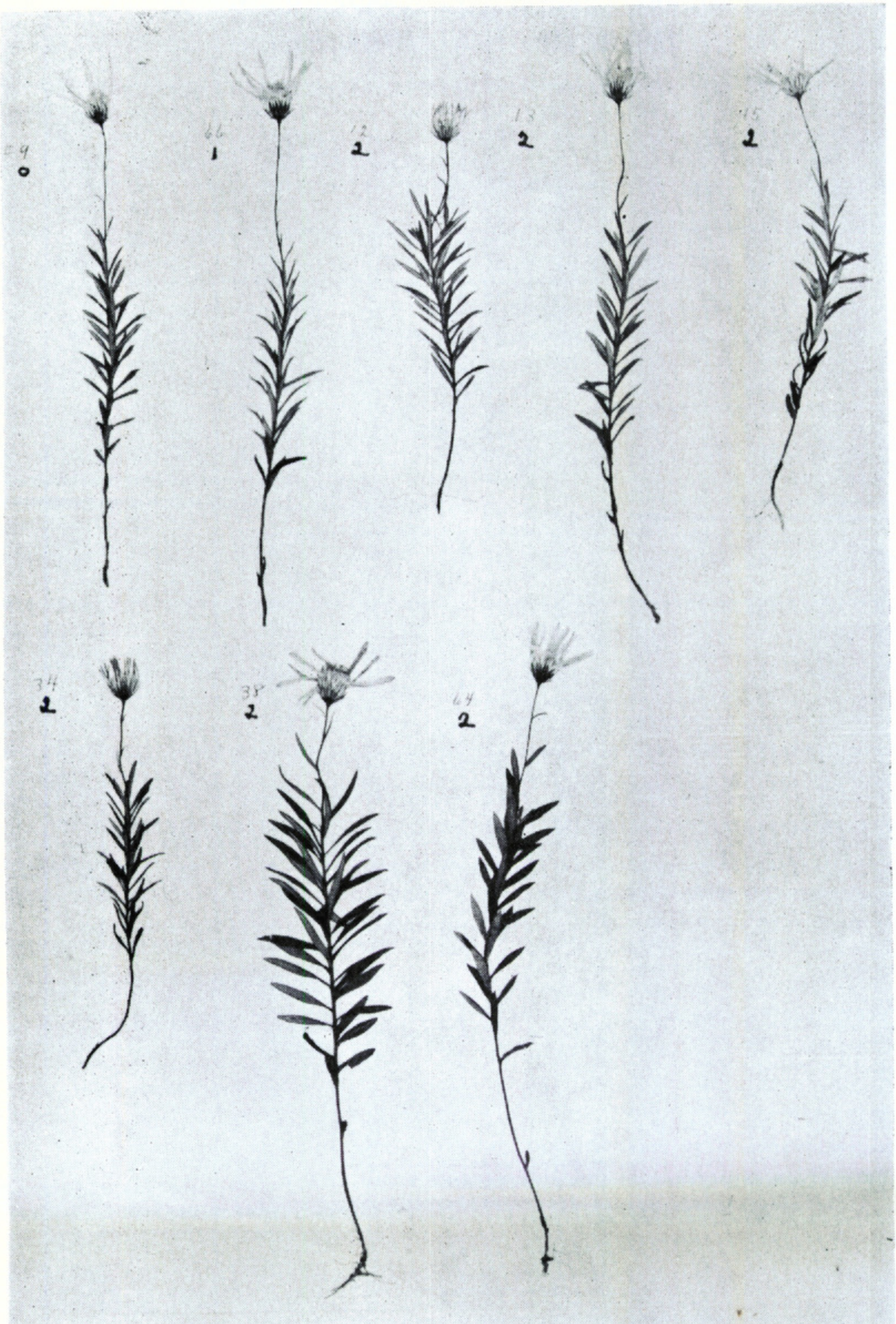

Figure 9.

Specimens scoring 0 to 2 on the hybrid index from 1960 population collection of sixty-nine individuals, from Outer Wood Island, Grand Manan. All are excellent examples of *Aster nemoralis* showing expected intraspecific variation.

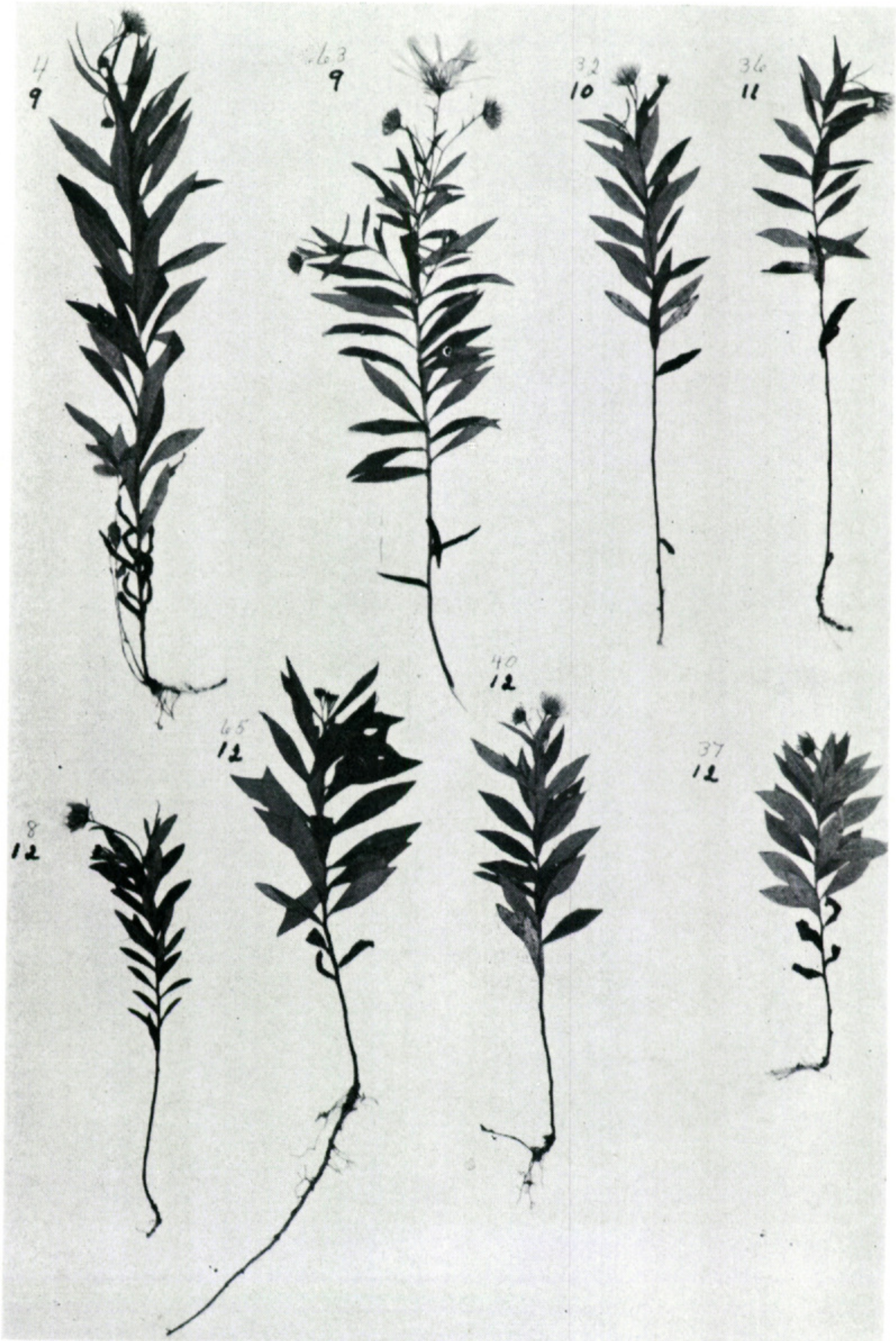

Figure 10.

Specimens scoring 9, 10, 11 and 12 on the hybrid index showing characters intermediate between the plants shown in Figures 9 and 11. They key as *Aster* × *Blakei.*

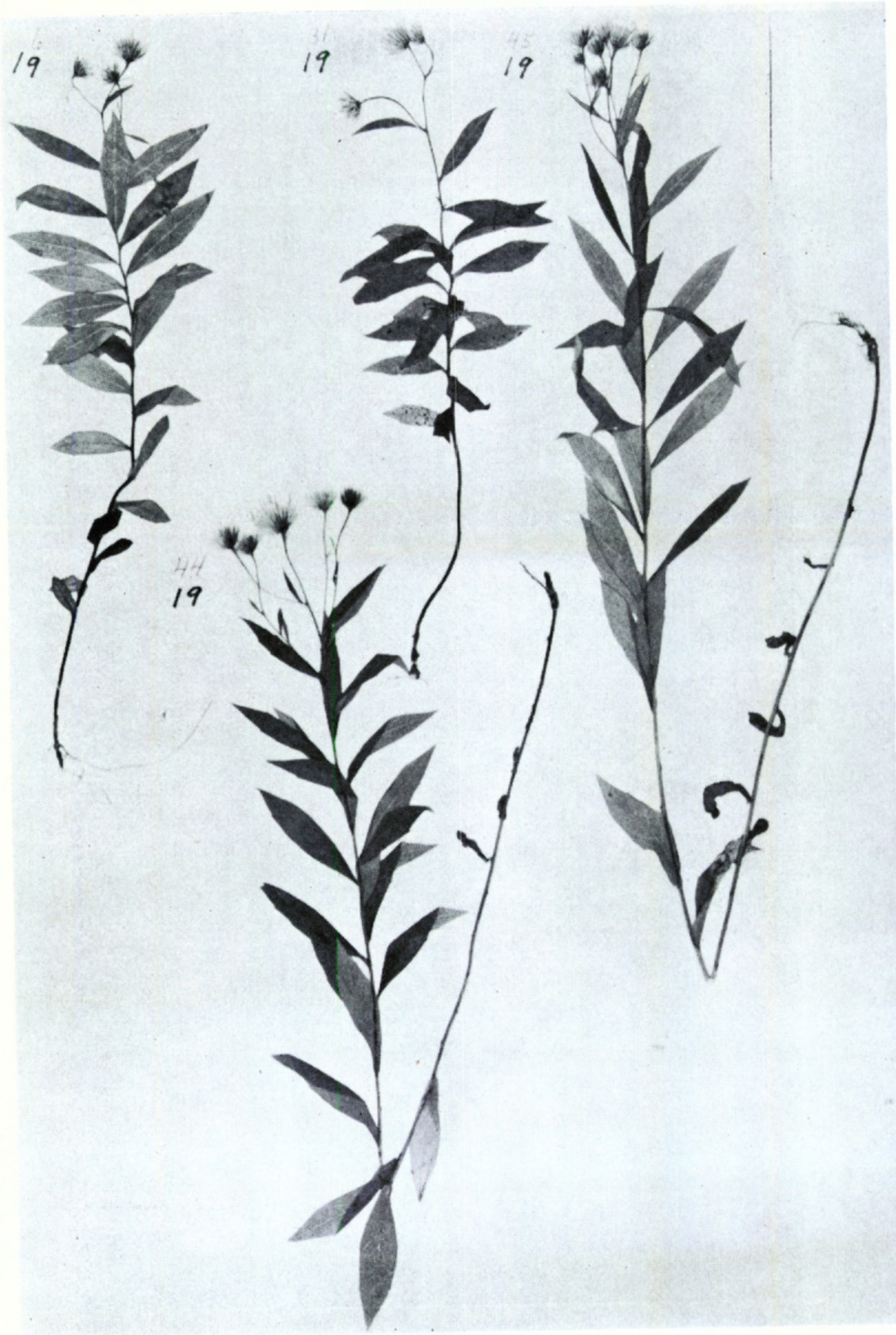

Figure 11.
Asters scoring 19 on the hybrid index show strong influence of both parents and are properly classed as *Aster* × *Blakei.*

Figure 12.

Plants scoring 25 on the hybrid index fall within the range of *Aster acuminatus* and key to this species in Gray's Manual of Botany, 8th edition. These specimens are from the same original population as those shown in Figures 9, 10 and 11 and are the extremes on the *A. acuminatus* end of the scale.

or no shade competition except from low thin sedges, while *A.* × *Blakei* being taller and more shade tolerant and vigorous endures the competition of subshrubs, grasses and sedges at the first part of the transition zone. Moreover segregates contiguous to *A. nemoralis* physically seemingly approach it also in tolerance of habitat wetness and can thus compete in wet boggy areas with taller vegetation of possibly up to two to three feet. Where the abrupt change to taller shrubs occurs with their dense growth, suitable habitats cease. Not until the forest margin do suitable habitats for *A. acuminatus* appear. Thus the ecological niches of *A. nemoralis* and *A. acuminatus* are almost invariably separated. Where *A. Blakei* occurs, it must mean that at some time the two areas adjoined one another and hybridization occurred. The survival of *A. Blakei* can be attributed to its moderate tolerance of wetness and its superior stature and vigor. Subsequent changes allowing the penetration and development of tall shrubs would eliminate *A. acuminatus* leaving the hybrid with its superior capacity for spreading by rhizome extension on the bog margins with opportunity to backcross to *A. nemoralis*. Without question, this is the explanation of the existence of populations such as those at Ethan Pond and other inland stations where *A.* × *Blakei* is found associated only with the *A. nemoralis* parent.

The pattern of transition from wet sphagnum bog to coniferous forest breaks down on the coast of eastern Maine and the Bay of Fundy. Here in the saturated atmosphere of that foggy climate, the sphagnum of the bogs may invade and even destroy the coniferous forest, frequently with little or no transition zone of sedges and shrubs. Here the ecological requirements of both parental species coincide allowing hybridization and continued survival of parents and progeny.

Both *Aster acuminatus* and *A. nemoralis* have become adapted to highly specialized habitats; habitats, moreover, that must have long existed in the mesic forests and bogs of the east and northeast, fluctuating with glacial advance and retreat. Only rarely, would such contrasting habitats coincide and the conditions of coincidence must have borne close resemblance to the cold maritime sites of Outer Wood Island, Great Wass Island, Mistake Island and to the montane locations of Ethan Pond and Chocorua Lake. The ecological similarity of montane sites and sea level bogs is noteworthy and is especially high-lighted by an as yet unpublished study by Teeri, et al, on Campobello Island, New Brunswick. Within the overlapping ranges of *A. acuminatus* and *A. nemoralis*, such ecologically exacting sites must have repeatedly occurred during Pleistocene advance and retreat. With ecological barriers thus removed, genetic compatibility becomes evident with the appearance of the *Aster* × *Blakei.*

With vigorous vegetative propagation by far ranging rhizomes inherited from both parents and adaptation to a hybrid habitat, *Aster* × *Blakei* was in a position to survive without direct competition with either parent. With at least some genetic compatibility allowing backcrossing, *A.* × *Blakei* was in a position to maintain itself once the initial interspecific crossing was accomplished. With changing conditions, the specialized environments of one or both parent species could be wiped out, leaving *A.* × *Blakei* alone in its less vulnerable habitat, or with one or the other of its parents. The fact that it has been found with one parent more often than the other can be explained by postulating either greater genetic compatibility in one direction than the other or a greater availability of suitable environment in one direction than the other or a combination of both factors.

ASTER × BLAKEI

Representative Specimens

The following specimens have been selected from all over the recorded range of *Aster* × *Blakei.* They have been examined and verified as meeting the description and falling within the hybrid index values of *A.* × *Blakei.*

CANADA: NEWFOUNDLAND: Port aux Basques, *Fernald, Long & Dunbar* 27141 (GH).

NOVA SCOTIA: CAPE BRETON: VICTORIA CO., St. Paul Island, *Perry & Roscoe* 397 (GH); North Sydney. *Bissell & Linder* 22812 (GH);
GUYSBOROUGH CO., West Cook's Cove, *Perry & Wetmore, Hicks & Pringle* 10017 (GH); Canso, *Fowler* 8801 (GH);
HALIFAX CO., Halifax, *Howe & Lang* 1506 (GH);
ANNAPOLIS CO., Liverpool Head Lake, *Fernald & Long* 22462 (GH);
QUEENS CO., Broad River, *Fernald & Bissell* 22811 (GH);
SHELBURNE CO., Shelburne, *Fernald & Long* 24660 (GH);
YARMOUTH CO., *Fernald, Long & Linder* 22813 (GH);
DIGBY CO., Haverlock, *Fernald & Long* 24661 (GH); Brier Island, Western Point, Aug. 19, 1962, *Hodgdon, Hodgdon, Pike & Denbow* (NHA).
NEW BRUNSWICK: CHARLOTTE CO., Wolf Islands, East Wolf, Southwest Cove, Sept. 19, 1964, *Burns, Hodgdon, Hodgdon, Pike & Saltonstall* (NHA). Grand Manan, Outer Wood Island, Aug. 21, 1963, *Pike & Pike* (NHA).
UNITED STATES: MAINE: FRANKLIN CO., New Sharon, Aug. 10, 1902, *Knowlton* (NHA);
OXFORD CO., Adamstown, *Pease* 26458 (NEBC); Waterford, Bog Pond, Aug. 16, 1883, *J. Blake* (MAINE);
WASHINGTON CO., Marshfield, *Knowlton* s.n. (NEBC); Roque Bluffs, July 27, 1913, *Knowlton* (NHA);
HANCOCK CO., Mt. Desert Island, Great Pond, Sept. 31, 1895, *Faxon* (GH); Broad Cove, Sept. 13, 1894, *Rand* (NEBC);
KNOX CO., Isle au Haut, Sept. 12, 1968, *Hodgdon* (NHA);
LINCOLN CO., Boothbay, Ocean Point, *Fassett* 2956 (NEBC); Southport, July 31, 1894, *Fernald* (NEBC);
KENNEBEC CO., Monmouth, Sept. 25, 1896, *Fernald* (NEBC);
SAGADAHOC CO., Topsham, *Bean* s.n. (NEBC);
ANDROSCOGGIN CO., South Poland, 1895, *Kate Furbish* (NEBC);
CUMBERLAND CO., Baldwin, *Fernald, Long & Norton* 14478 (NEBC); Otisfield, Moore Pond, Aug. 1958, *J. Blake* Bowdoin Collection (NHA);
YORK CO., Limington, *Fernald, Long & Norton* 14747 (NEBC); Wells, Aug. 1849, *J. Blake* Bowdoin Collection (NHA).
NEW HAMPSHIRE: CARROLL CO., Wolfeboro, Carrying Place, Aug. 27, 1909, *Sargent* (NHA); Tamworth, Chocorua Lake, Sept. 21, 1865, *J. Blake* Bowdoin Collection (NHA); Ossipee, *Pease* 30386 (NEBC);
GRAFTON CO., Bethlehem, Ethan's Pond, *C. & E. Faxon* 82777 (GH); Livermore, Aug. 15, 1948, *M. Gale* (NHA); Enfield, *Kennedy* 8390 (NEBC).
STRAFFORD CO., Madbury, *Hodgdon, Hehre, Teeri & Bruns* 14576 (NHA); Somersworth, *Hodgdon & Giddings* 4944 (NHA); Strafford, *Hodgdon* 2918 (NHA);

BELKNAP CO., Gilmanton, Shellcamp Pond, Aug. 28, 1876, *J. Blake* (MAINE);

MERRIMAC CO., Hooksett, Aug. 24, 1925, *Batchelder* (NHA);

ROCKINGHAM CO., Northwood, *Pease* 31793 (NEBC); Deerfield, *Pease* 31784 (NEBC);

HILLSBORO CO., Hancock, Sept. 7, 1963, *Patricia Stocking* (NHA); Peterboro, Sept. 2, 1901, *Williams* (NEBC);

CHESHIRE CO., Rindge, Sept. 14, 1913, *Forbes* (NEBC); Jaffrey, *Robinson* 82898 (GH).

VERMONT: ESSEX CO., Brunswick, *Pease* 29324 (NEBC);

LAMOILLE CO., Johnson, Belden Pond, Sept. 1, 1894, *Grout* (GH).

MASSACHUSETTS: ESSEX CO., Gloucester, Aug. 30, 1881, *Swan* (NEBC); Hamilton, *Hunnewell* 4630 (NEBC);

MIDDLESEX CO., Chelmsford, Sept. 20, 1902, *Knowlton* (NEBC); Bedford, Oct. 1896, *Jenks* (GH);

PLYMOUTH CO., Wareham, *S. F. Blake* 10751 (GH); East Wareham, *Griscom* 12767 (NEBC);

WORCESTER CO., Uxbridge, *A. Gray* 3282 (GH); Hubbardston, Sept. 9, 1940, *Weatherby & Rollins* (NHA).

RHODE ISLAND: WASHINGTON CO., South Kingston, *Griscom* 24023 (NEBC); Hopkinton, *Lownes* 466 (GH);

KENT CO., East Greenwich, *Congdon* 4697 (MAINE).

NEW YORK: HERKIMER CO., Big Moose Station, July 12, 1899, *Peck* (GH); Five Ponds, Aug. s.n., *Chas. H. Peck* (N.Y.S.)

HAMILTON CO., Lime Kiln Lake, *Wiegand* 16762 (GH);

ST. LAWRENCE CO., Clifton, *Wright* 13042 (GH).

NEW JERSEY: OCEAN CO., Egg Harbor, Sept. 19, 1897, *Pollard* (GH); Lakewood, *Hunnewell* 6335 (GH).

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The Bowdoin collection now on ten year loan to the University of New Hampshire Herbarium has been remarkably

valuable as it contains specimens collected by the Rev. J. Blake who over 100 years ago recognized the position of the aster later named for him.

The graphic diagrams in Figs. 1, 2 & 3 were constructed by Norman Reynolds of the Botany Department, and the photographs of specimens were made by staff of the Photographic Department both of the University of New Hampshire.

Constant associate and mentor in this study Albion R. Hodgdon, Curator of the Herbarium of the University of New Hampshire.

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LITERATURE CITED

AVERS, CHARLOTTE J. 1953. Biosystematic studies in Aster. I: Crossing Relationship in the Heterophylli. Am. Jour. Bot. **40:** 669-675.

——————— 1953. Biosystematic studies in Aster II: Isolating mechanisms and some phylogenetic considerations. Evolution 7: 317.

ANDERSON, E. 1936. Hybridization in American Tradescantias. Ann. Missouri Bot. Gard. **23:** 511-525.

——————— 1949. Introgressive Hybridization. Wiley & Sons, New York. pp. 109.

FERNALD, M. L. 1933. Recent discoveries in the Newfoundland Flora. Rhodora **35:** 5.

——————— 1949. Gray's Manual of Botany, 8th ed.

——————— 1949. Studies of Eastern American Plants. Rhodora **51:** 99-100.

——————— 1921. Expedition to Nova Scotia. Rhodora **23:** 156-295.

GRAY, ASA. 1887. Gray's Lessons and Manual of Botany, revised edition. Ivison, Blakeman and Company, New York. pp. 40 & 42-44.

HOUSE, H. D. 1919. Notes on local floras. VI. N. Y. State Museum Bull. **241:** 219-220.

JENNINGS, O. E., ANDREY AVINOFF. 1953. Wild Flowers of Western Pennsylvania and the Upper Ohio Basin. Vol. II. Plate 178. Univ. of Pittsburgh Press.

MACOUN, JAMES M. 1896. List of the Plants known to occur on the Coast and in the Interior of the Labrador Peninsula. (Reprinted from Annual Report, Geological Survey of Canada.) Vol. VIII., Part 1, Appendix VI: 3531-3661.

PORTER, THOS. C. 1894. *Aster nemoralis Blakei.* n. var. Bull. Torr. Bot. Club **21**: 311.

ROLAND, A. E. 1945. The Flora of Nova Scotia. Truro Printing & Publishing Co., Truro, N. S.

ROSENDAHL, C. O. and ARTHUR CRONQUIST. 1949. Asters of Minnesota: A Floristic Study. Am. Midl. Nat. **42**: 502-512.

SEYMOUR, F. C. 1969. The Flora of New England. Charles E. Tuttle, Rutland, Vt.

SHINNERS, L. H. 1941. The Genus Aster in Wisconsin. Am. Midl. Nat. **26**: 398-420.

——————— 1943. The Genus Aster in Nova Scotia. Rhodora **45**: 344-351.

STEBBINS, G. L. 1950. Variation and Evolution in Plants. Columbia University Press, New York.

TORREY, JOHN and ASA GRAY. 1841. A Flora of North America. Vol. II: Wiley & Putnam, New York. 157-158.

WEATHERBY, C. A. and JOHN ADAMS. 1945. A List of the Vascular Plants of Grand Manan, Charlotte County, New Brunswick, Contrib. Gray Herb. CLVIII.

WIEGAND, K. M. 1928. Aster lateriflorus and some of its relatives. Rhodora **30**: 161-162.

——————— 1933. *Aster paniculatus* and some of its relatives. Rhodora **35**: 16-19.

WETMORE, R. H. and A. L. DELISLE. 1939. Studies in the genetics and cytology of two species in the genus *Aster* and their polymorphy in nature. Am. Jour. Bot. **26**: 1-12.