Rhodora

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THE ECOLOGY OF THE NATURAL ORIGIN OF A SPECIES OF CAREX BY HYBRIDIZATION

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In the upper Kuskokwim River Region of Alaska, there is a population of *Carex* which seems to be of hybrid origin. I feel that the biology of this population indicates that it has reached species status, because it fruits abundantly over a wide area and maintains its identity both in the presence and absence of the suggested parental species, *Carex rotundata* Wahlenb. and *Carex rostrata* Stokes.

The population appears in a mixed environment which is produced when sphagnum bogs invade sedge swamps coincident with special soil processes related to the age of the floodplain and to the conditions of perennially frozen ground. In the environment thus created the hybrid population has had partial ecological isolation and seems to have persisted by vegetative reproduction until sexual reproduction has become established. The population has thereby become independent of resynthesis and is genetically integrated.

In a paper that will appear as *Contributions from the Gray Herbarium of Harvard University*, No. 178, I have described the changes in the alluvial deposits and the vegetation on the floodplain of the Upper Kuskokwim River. The physiographical and botanical processes briefly treated here are discussed in detail in that paper.

The Floodplain and Its Vegetation

On the youngest parts of the floodplain of the Kuskokwim River there is a tall forest of Balsam Poplars (*Populus balsamifera*), White Spruce (*Picea glauca*), or White Spruce mixed with White Birch (*Betula papyrifera*). On the flooded shores of sloughs, ox-bows and bar lakes in this well-drained area there are zonations of vegetation from emergent grasses and sedges to willows. *Carex rostrata*, one of the putative parent species, grows just at the upper limit of average water-level in shallower water than *Carex aquatilis* and *Glyceria* and on wetter places than *Calamagrostis canadensis*.

The older parts of the floodplain have a thick carpet of moss the insulating effect of which leads to the preservation of frozen ground and the accumulation of surface water. The oldest floodplain surfaces have a forest of Black Spruce (*Picea mariana*) and a floor of sphagnum. Scattered in this forest are many large bogs. These bogs are of a treeless peat bog type characterized by an abundance of sedges, including *Carex rotundata*, the other putative parent of the new species. The zones of different age of the floodplain merge into each other and between the youngest and the oldest is a broad zone of transition both in the vegetation and in the conditions of the alluvium. Over most of this older part of the floodplain, bogs are actively invading ox-bow and bar lakes, swamping the forest floor and thawing into the frozen subsoil undermining and destroying the forest. Shallow lakes and sloughs have been initially bordered by the vegetation of silt shores, then peat mosses have colonized and have replaced the shore vegetation. The combination results in a mixed environment and, as would be expected in such an unstable environment, species of sphagnum and higher plants appear which are not present in either the pure peat bog or the pure mineral silt environment. Such species are, for example, *Sphagnum teres*, *S. Ångströmii*, *S. recurvum*, *S. riparium*, *S. robustum*, *S. fimbriatum*, and *S. plumulosum*, *Carex chordorrhiza*, *C. tenuiflora*, *C. canescens* var. *subloliacea*, *C. magellanica*, *Cicuta mackenzieana*, *Chamaedaphne calyculata* var. *angustifolia*, *Galium tinctorium* and *G. Brandegei*. In such areas where bogs invade a silt-bottomed pond, *Carex rostrata* occurs on the silt shores and *Carex rotundata* in the peat bog. Between them is a large unstable area where the area available for growth of any individual is nearly unlimited, and vegetative reproduction is widespread.

In such areas, where peat bogs are invading sedge sloughs, I have collected a plant which is intermediate between *Carex* *rostrata* and *Carex rotundata.* Because of the forces active in modifying the wet lands of the Upper Koskokwim River lowlands, invading bogs are more widespread than either "typical" type and the intermediate plant, named here *Carex paludivagans*, is more common and widespread than either of the "parent" species. These plants are readily recognized by their folded, stiff and coarse leaves and two rather dense pistillate spikes containing tightly packed, brownish perigynia.

The various alternative explanations of this population are: a) that this population is an extreme variant of one parent released under special conditions of the habitat, b) that it is a separate species which had an origin independent of *C. rostrata* and *C. rotundata*, c) the parents and the present population are all variants of the same species, d) that this is a population intermediate between the two "parent" populations and not a separate species.

In the following pages reference will be made to certain numbers such as *3271*, *4659*, or *1667*. These are the field numbers assigned to specimens when collected and recorded in a field catalogue. Such numbers represent a single collecting site and 10–15 plants collected at that site. Each is a single sample of a local population.

Carex paludivagans

In the course of the field work this apparently quite distinct population was considered a separate unidentified species and, as a result, proper mass collections were not made. Furthermore, the newly synthesized populations represented in field numbers *3263* and *3265* were not appreciated to have any application to this complex.

Final studies have shown that all of the characters of the large intermediate population lie well within the extremes of variation expressed in the two parents, as shown in Table 1. The habitat itself presents a blending of the parental physiological requirements and is an unstable habitat in keeping with studies of hybrid populations made by others. The possibility remains, of course, that I have not been able to find the particular characters which might show an origin completely independent of the suggested parents, but this is unlikely since a systematic review of all the features usually used in descriptions of *Carex* was made in com-

TABLE 1A

TABULATION OF CHARACTERISTICS

	C. paludivagans	**3263 (pt), 3265**	**2084, 3263 (pt)**	**4341, 2169**
Habitat	mixed bog and silt shore	edge of bog-invaded slough	edge of bog-invaded slough	edge of bog-invaded lake
Plant height—cms.	(40)45–50(60)	55–85	50–80	42–65
Plant base	rather coarse and soft	coarse and soft	coarse, soft, shoots reddish	coarse, soft, shoots reddish tinged
Leaf width—mms.	1–2.5	1–2.5	5–7	3–4
Leaf character	folded glaucous	folded to involute	flat grey-green	flat, grey-green
Septate nodulose	obscurely to conspic.	conspicuously	conspicuously	conspicuously
Inflorescence length—cms.	5–17	(8)10–12(18)	18–23	(10)15–18(23)
No. male spikes	1–3	1–3	2–4	2–3
Longest male spike—mms.	22–45	26–38	38–54	25–60
No. female spikes	(1)2	1–2	2–3	2–3
Longest female spike—mms.	11–35	(14)20–30(35)	23–58	25–55
No. perigynia in longest spike	(40)60–80(90)	34–120	87–145	63–140
Arrangement in spike	packed to rather loose, ascending to spreading	tightly packed, spreading	tightly packed, squarrose	loosely packed, ascending
Perigynium shape	elongate oval tapering to beak	obovate, abruptly beaked	ovate, plump at base tapering to beak	broadly oval or ovate, rather abruptly beaked
Perigynium length—mms.	4–4.5	3–4.3	4.5–5.2	3.5–4
Beak length—mms.	1–1.5	0.2–0.4	1.1–1.6	0.4–0.8
Beak teeth, length	0.1–0.2	0.1–0.2	0.2–0.6	0.1–0.3
Beak teeth	acute	blunt to acute	acute to acuminate	acute to acuminate
Female scale	blunt to acuminate	acute to long acute	abruptly acute, aristate	narrowly acute
Perigynium color	straw or tan, brown or dark brown apex and beak	yellow brown with occasionally dark brown apex and beak	straw color with brown apex and beak	yellowish tan with often darker apex and beak
Perigynium texture	membranaceous	membranaceous	membranaceous	stiffly membranaceous
Perigynium stalk	absent	absent	absent	nearly absent
Color of female scale	pale purplish brown, hyaline margin and midrib	pale purplish brown, hyaline margin, light midrib	reddish brown, hyaline margin and light midrib	purple brown with narrow hyaline margin and light midrib
Lowest bract	ascending spreading	ascending	ascending	ascending
Width of lowest bract—mms.	1.5–2	1–3	4–5	2–2.5

TABLE 1B

TABULATION OF CHARACTERISTICS

	C. rotundata	3844	C. membranacea	3819, 3820	C. rostrata
Habitat	Sphagnum-sedge meadow	wet sphagnum-sedge slope	wet mineral soil	wet sedge-moss slope	silt pond shores
Plant ht.—cms.	(15)25–30(40)	29–32	25–42	32–35	(60)80–100(120)
Plant base	slender, stiff brown	slender, rather stiff, brown	coarse, rather soft, reddish	coarse, soft reddish brown	coarse, soft, shoot reddish tinged
Leaf width—mms.	1	1	3–4	3.7–4.2	4–8.5
Leaf character	involute glaucous	involute glaucous	flat, green	flat gray-green	flat, gray-green
Septate nodulose	obscurely	obscurely	obscurely–conspic.	conspicuously	conspicuously
Inflorescence length—cms.	3–8	3.5–7.5	(3)4.5–6(12)	(5)7–9(12)	13–*18*–30
No. male spikes	1(2)	(1)2	(1)2	(1)2(3)	3
Length of longest male spike—mms.	12–26	17–24	(9)16–20	20–35	36–*44*–95
No. female spikes	1(2)	1–2	(1)2(3)	(1)2(3)	2–4
Length of longest female spike—mms.	7–13	10–15	(15)20–30(45)	(10)25–30(40)	21–*32*–75
Perigynia per longest spike	(20)–*35*–(45)	(21)28–36	42–*58*–65	(42)70–100(141)	(90)140–180(210)
Arrangement in spike	packed to rather loose, spreading	rather loose, ascending spreading	rather loose, spreading	rather loose, ascending spreading	loose, ascending to slightly spreading
Shape of perigynium	oval, abruptly beaked	ovate to orbicular, abruptly beaked	oval to ovate abruptly beaked	ovate tapering to beak	oval to lanceolate tapering to beak
Perigynium length—mm.	3–3.5	2.3–3	2.5–3	4–5	5–*6.5*–12
Beak length—mm.	0.2–0.5	0.5	0.5	0.8–1	1.5–2.0
Beak teeth—mm.	0.1–0.2	0.1	0.2–0.3	0.1–0.2	0.4–0.7
Beak teeth	blunt	blunt	acute to narrowly acute	acute to narrowly acute	acute to narrowly acute
Female scale	acute	acute-acuminate	narrowly acute	acute to narrowly acute	acuminate to aristate
Perigynium color	tan	tan to purplish	purplish	tan to tan with purplish apex	tan to pale brown
Perigynium texture	rather indurate	membranaceous	membranaceous	membranaceous	rather indurate
Perigynium stalk	absent	present	present	present	nearly absent
Color of female scale	tan	purple-black	purple-black	purple-black light midrib	dark, purplish brown, light margin, occasionally midrib
Lowest bract	**divergent**	ascending	ascending	ascending	ascending
Width of lowest bract—mm.	1	1	2	3	3.5–4.5

paring the three populations involved and in writing a description of the new species.

The second alternative explanation of this population is that it is an extreme variant of one of the parents elsewhere suppressed by competition. The two parent species occur all across Europe from northern Scandinavia across Siberia to Alaska and Greenland. In Asia *C. rostrata* occurs south to Kashmir and Korea. In North America it occurs all across the North and south to Utah and Delaware. In Siberia *C. rotundata* occurs south only to 61° north, but is in the Altai Mountains and Sakhalin. In the New World it is known from Alaska. There is doubt that the plants reported from Greenland and the Labrador coast as this species are separable from the Eurasian *C. saxatilis* (Polunin 1943). Since the parental species occupy largely the same area in the circumboreal region it would not be justified to suggest that this population be an extreme variant. If such a variant occurred here it should occur in many places in the range of the parent species where their ranges do not overlap geographically or ecologically.

It is possible that the parents and this population are all variants of the same species, the third alternative, but the diagram of character index (Figure 1) and drawings of the perigynia (Figure 2) show the presence of three clearly unified aggregations of characters. These exist together in one area. If these were indeed variants of the same species it would go against all experience of field naturalists and what is known at present of the nature of species barriers and the maintenance of population integrity. If similar occurrences that are found in other parts of the range are considered, *Carex saxatilis, C. physocarpa, C. rostrata, C. rotundata,* and *C. membranacea* would then all have to be included in one polymorphous species.

There remains the possibility that this is indeed a hybrid population, but one which has not the identity nor the integrity of a species. This is the most serious objection to the naming of this population as a species, and one that can only be answered by qualitative arguments.

Seeds were brought back and germination tests made, but these failed. No seeds of either "parent" or of *C. paludivagans* germinated. Forty to sixty per cent of the perigynia, however,

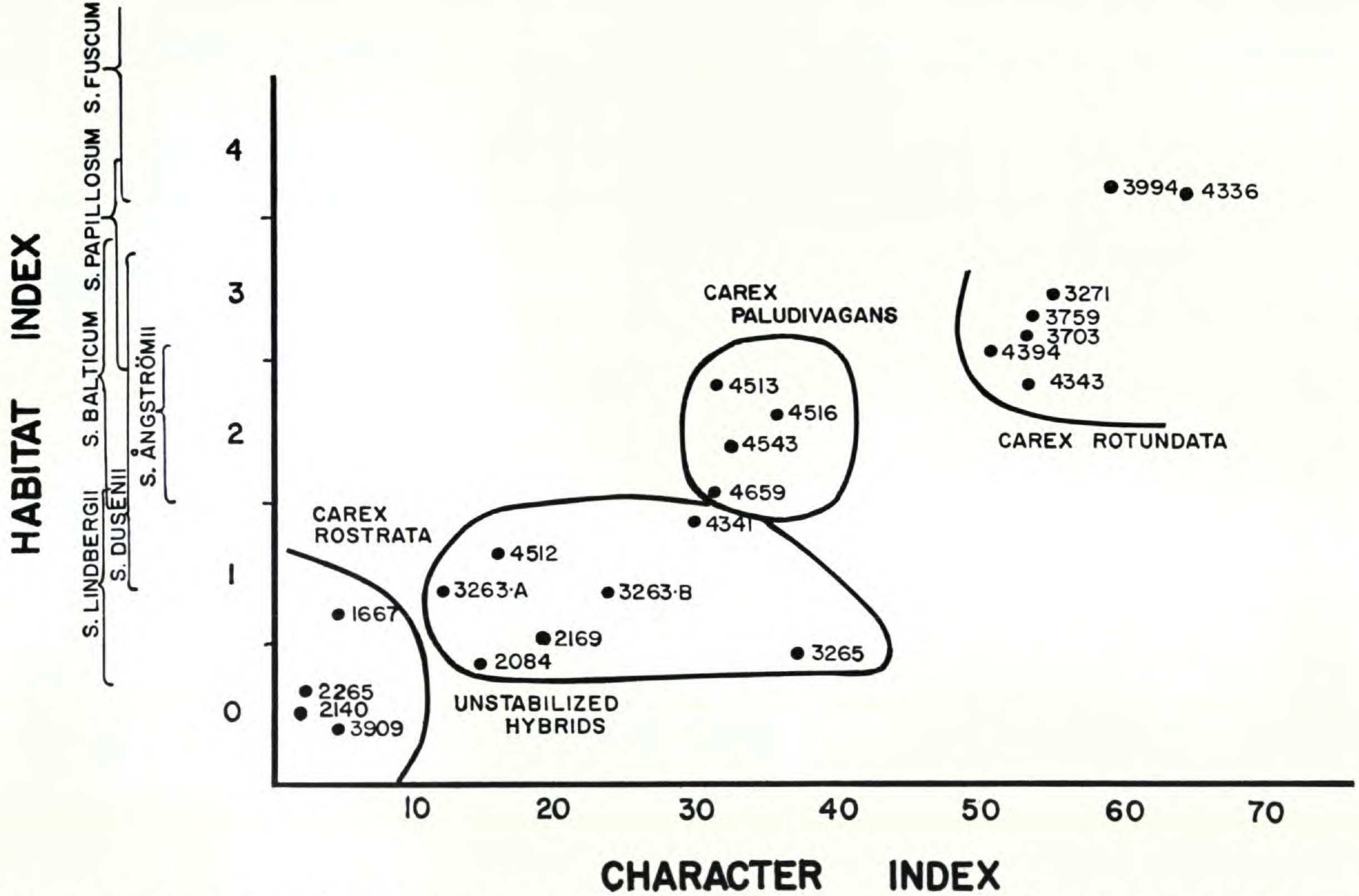

FIGURE 1. Species characteristics plotted against habitat. The individual morphological characters are given a numerical value according to Table 2, and their sum plotted against the spectrum of habitat variation. *Carex rostrata* collections appear on the bottom left of the plot and *Carex rotundata* collections on the top right. *Carex paludivagans* appears in the middle, partially separated from the recent hybrids.

contain achenes that are normal in appearance, not shriveled, and as large as those of the "parents." In one collection, anthers were found containing a mass of shriveled, presumably sterile, pollen but plump pollen grains that stained deeply with lacto-phenol and cotton blue were also found on the same specimen. Most of the pollen, of course, had been shed by the time the ripe perigynia represented in my collections were formed, but one or two plump pollen grains that stained could be found on each collection sheet of *C. paludivagans*.

In most bogs *Carex paludivagans* and *Carex rotundata* were abundant and *Carex rostrata*, although very localized, could be found in isolated reëntrants. In most of the bogs where all three occurred, the populations were quite distinct, but in several cases part of the bog on the border of a stand of one parent had a very variable, sterile and evidently hybrid intermediate stand. In some parts of the valley, intermediate populations were not seen to fruit, but reproduced actively by stolons. In these places the population was probably made of more or less sterile clones from recent hybrid seedlings. Over most of the bog area, however, plants of *C. paludivagans* fruited abundantly, and in three large bogs, I could not find either parent although *C. paludivagans* was present in large numbers and was fruiting abundantly (producing 80% filled achenes). Over most of the valley *Carex paludivagans* is more abundant and widespread than either or both the parents. On this basis I suggest that the population deserves recognition as a species.

These plants have "taken advantage" of the ability of the hybrids to persist by vegetative reproduction until chance rearrangements of genes or chromosomes and environmental selection allowed sexual reproduction to occur and a balance of characters suitable to the habitat to emerge. The widespread asexual reproduction provides increased chances for such rearrangements to a balanced gene system. The constant renewal of the unstable habitat leads to resynthesis of the hybrid many times. Long life and asexual reproduction have greatly increased the chances of survival and the ultimate success of a hybrid of this type, while such a population among short-lived, usually only sexually reproducing, animals would be doomed before chance rearrangements toward fertility occurred.

Detailed Analysis of the Characters

Figure 2 shows drawings of samples of perigynia and pistillate scales from the field collections that will be discussed in the following paragraphs. In several places where both parents are numerous and grow very close together, a very variable intermediate population has been found between them (vis. 3263-A, 3263-B, 3265; Fig. 2). In most other areas a homogeneous population occupies a large area relatively isolated from the parents. To test whether there is any reality to the impression that there is an integrated separate population, a character index was constructed similar to that used by Anderson and Hubricht (1938) or Sibley (1954). The 16 characters rated were plotted against habitat and habitat was classified according to position in the spectrum from swamp to bog, and to degree of disturbance. Figure 1 shows the result of this tabulation. In it ideal *C. rostrata* would have a value of 0 and ideal *C. rotundata* have a value of 64. The characters used and the values assigned are documented in Tables 1 and 2 since in constructing an index such as this there is danger that in the selection, values assigned are biased toward producing the desired results. Particular values assigned each character of all the field collections are shown in Table 3.

Four divisions of habitat were erected for classification of the habitat as follows:

0 : silt shores of an ox-bow or bar lake located in the White Spruce and deciduous forest.

1 : shore of an ox-bow bog or pond recently invaded by bog sedges and mosses; silt is found in the roots of specimens; plants present include *Equisetum fluviatile, Potentilla palustris, Sphagnum Lindbergii, S. Dusenii,* and species of *Drepanocladus* and *Calliergon.*

2 : wet sedge-meadow of a deep bog on the margin of a lake or deep pond invaded by bog vegetation characteristically accompanied by *Sphagnum balticum, S. Dusenii, S. recurvum, S. riparium, S. Ångströmii, S. teres,* and *Carex chordorrhiza.*

3 : Wet sedge meadow in *Strangmoor* areas, or on the upper parts of flat bogs which have advanced by swamping up a drainage, characteristically part of a simple association with sphagnum (*Sphagnum balticum, S. Dusenii, S. papillosum, S. pulchrum, Carex limosa* and occasionally *C. rotundata*).

4 : dry sedge-meadow or a shallow isolated pot hole; *Sphagnum papillosum* and scattered *Andromeda* and *Myrica.* Where this is drier *Drosera rotundifolia, Chamaedaphne, Vaccinium uliginosum, V. Oxycoccus* and *Sphagnum fuscum* appear.

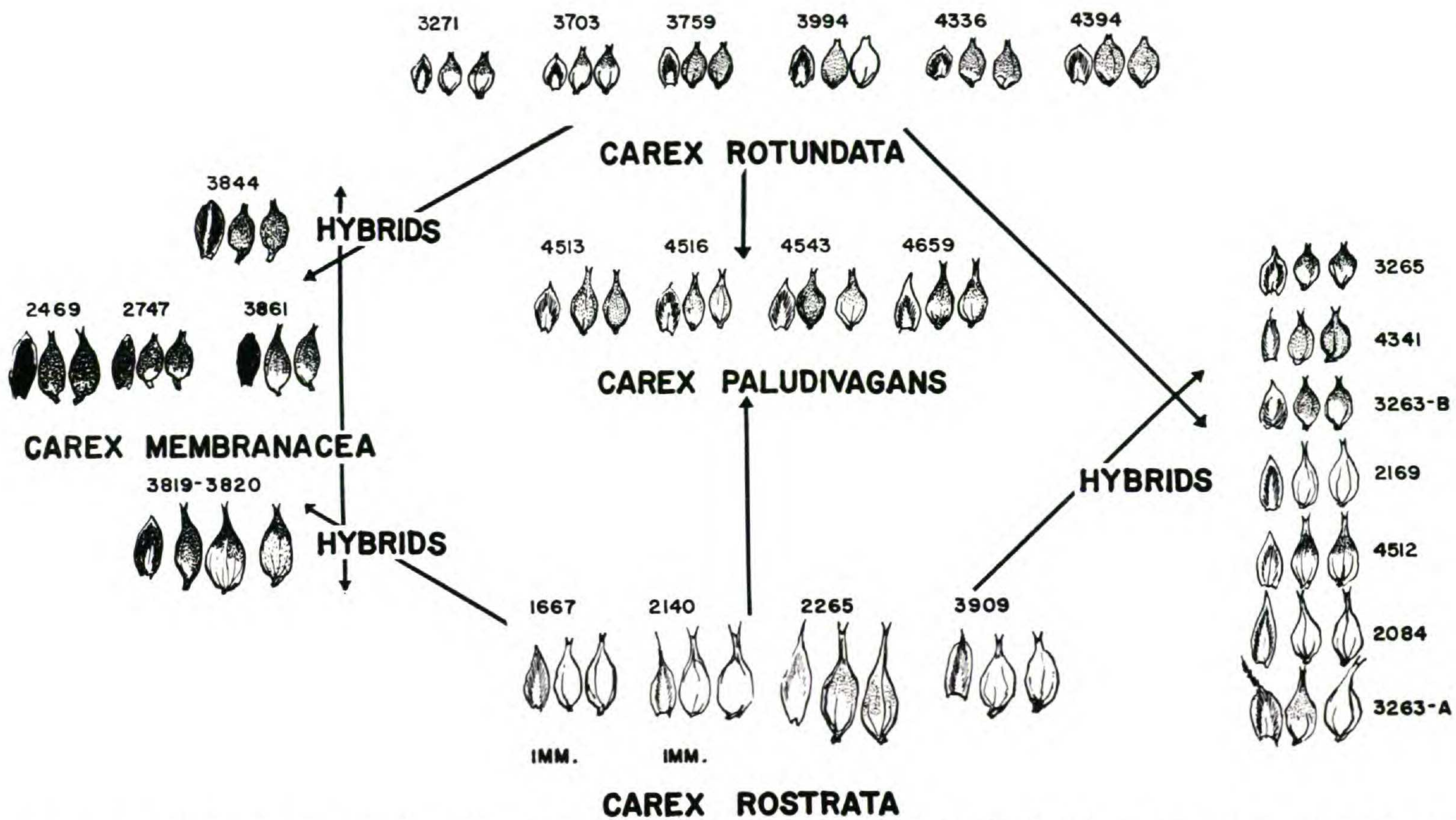

Figure 2. Perigynia and female scales. Field numbers are given above each illustrated sample. Recent hybrids are illustrated as well as the stabilized population.

TABLE 2

TABULATION OF CHARACTERS

Habitat	0	1	2	3	4
Height in cms.	80–120	60–80	45–60	30–45	15–30
Base of plant	coarse and soft	coarse, rather stiff	coarse-grasslike, indurated	coarse-grasslike, rather stiff	slender and stiff
Leaf width—mms.	4–8.5, flat	folded and flat	1–2.5, folded	folded and involute	1 or less, involute
Septate nodulose	conspicuously	most bases conspicuously	nodulose, but not conspicuously	most bases obscurely	obscurely
Inflorescence length in cms.	20–30	15–20	8–15	5–8	3–5
No. male spikes	3–4	2–4	2	1–2	1
Length of longest male spike—mms.	50–100	40–50	25–40	20–25	12–20
No. female spikes	3–6	2–4	2	1–2	1
Length of longest female spike—mms.	41–95	31–40	19–30	13–18	7–12
No. perigynia in longest spike	141–180	81–140	61–80	41–60	20–40
Perigynium shape	long oval to lanceolate, tapering to a beak	long oval, tapering to a beak	elongate oval more or less tapering to beak	ovate to elongate oval, beak clearly separate	oval to orbicular abruptly beaked
Perigynium length including beak in mms.	5–12	4.5–5	4–4.5	3.5–4	2.3–3.5
Beak length—mms.	1.5–2.0	1.3–1.8	1–1.5	0.5–1	0.2–0.5
Shape of female scale	narrowly acute to aristate	acuminate, with awn, variable	blunt to acuminate	blunt to acute	blunt
Color of perigynium	tan	tan, some perigynia with dark beaks	many tan, and many with a dark apex and beak	tan, most with a brown apex and beak	tan with dark brown apex and beak
Lowest bract width in mms.	ascending, flat: 3.5–4.5	2–3.5	ascending—spreading:1.5–2	0.25–1.5	divergent, involute: 0.1–0.25

TABLE 3

Field Number	2265	2140	3909	1667	3263A	2084	4512	2169	3263B	4341	4659	4513	4543	4516	3265	4394	4343	3703	3759	3271	3994	4336
Habitat	0	1	0	1	1	2	1	2	1	2	2	2	3	2	2	3	3	3	4	3	4	4
Base of Plant	0	0	0	0	0	1	0	0	1	1	2	2	2	2	2	3	4	3	3	3	4	4
Leaf width	0	0	0	0	0	0	0	1	0	1	2	2	2	3	2	3	4	2	3	4	4	4
Septate nodulose	0	0	0	0	0	1	0	2	0	1	2	2	2	2	2	4	4	4	3	4	4	4
Inflorescence length	0	0	0	0	0	1	1	2	1	2	2	2	2	2	2	3	3	4	3	4	4	4
No. male spikes	1	0	0	0	1	0	0	1	2	2	2	2	2	2	2	4	4	4	4	3	4	4
Length longest	0	0	0	0	1	1	2	0	1	2	2	2	2	3	2	3	3	4	3	4	4	4
No. female spikes	0	0	0	1	0	1	2	1	0	1	2	2	2	3	2	4	4	3	4	3	2	4
Length longest	0	1	2	2	1	1	1	2	2	3	2	2	2	2	3	3	4	4	4	4	3	4
No. perigynia	0	0	0	0	0	1	2	1	1	2	2	1	2	3	2	3	3	4	4	3	4	4
Perigynium shape	0	0	1	0	3	3	1	2	4	3	2	2	2	1	3	3	3	3	3	3	4	4
Perigynium length	0	0	0	0	0	1	1	1	4	3	3	2	2	2	3	3	4	3	3	3	4	4
Beak length	0	0	1	1	1	1	2	2	3	3	2	2	2	2	3	3	3	4	3	4	4	4
Shape female scale	0	0	1	0	1	1	2	1	1	1	1	2	2	2	1	3	3	3	4	4	4	4
Perigynium color	1	0	0	0	3	0	0	0	3	2	2	3	2	2	3	3	2	3	3	4	2	3
Lowest bract	0	0	0	0	0	0	1	1	0	1	2	2	2	2	1	2	3	2	3	2	3	4
Total	2	2	5	5	12	15	16	19	24	30	32	32	33	35	37	50	54	53	54	55	59	63

In selection of the habitat index a more or less arbitrary system, in part influenced by the Scandinavian system of classifying vegetation by indicator species, was set up. It was very clear during the field work that there were divisions of the sedge meadow vegetation in addition to the separation of this major type from other major types such as low shrubs, high shrubs, or shallow water with emergent aquatics. In other words, along the disturbance-gradient, clear-cut differences exist to separate a) the sedges growing on silt beaches of ponds b) the sedge meadows of fully developed peat bogs where the sphagnum is usually *S. papillosum* with patches or zones of invading *S. fuscum* and c) the areas of sedge-meadow rich in species of sphagnum and of higher plants. In addition to these major differences there are intermediate sedge meadow types. In the wetter conditions *S. Dusenii* (a dark deep brown sphagnum usually immersed) is especially characteristic and in drier places *S. balticum* (a lighter colored sphagnum usually emergent) is typical. In the field there are three clear divisions. Zones 1 and 3 are less clear. This bog structure has created a natural ecological isolation for the three populations.

It is interesting to realize that again in these bogs there occurs the phenomenon familiar to the botanical collectors that rare species occur together in an unstable habitat. Such unstable habitats are the familiar "good collecting areas". The ecological explanation used here is that unstable or new populations or ones of restricted variability occur in disturbed places. The widespread vegetation is of a few common highly succesful species of many, many more individuals. Unstable habitats are discussed by Anderson (1949) and are of course familiar sites for introduced and native plants to go weedy.

Interpretation of the Index

The indices show that the population of *C. paludivagans* is as uniform as those of its two ancestors (Fig. 1). It also shows a case, *4341*, of separate synthesis of another hybrid population similar in index although they "look" different. This collection, *4341*, was made 50 miles from the main valley floor in a bog-invaded pond, on wind-blown silt overlying moraine. The plants look like a delicate, small *C. rostrata*, having more dense spikes and partly folded leaves. It seems to me that this is a separate synthesis of a *C. paludivagans*-type population which does not match exactly. If *C. paludivagans* was hybrid in origin, as is supposed, this repetition of its formation would be expected to occur several times where proper conditions exist, as in this case and that of *3263–3265*. Numbers *3263–3265* were collected from a variable population closely associated with both parents in the bog across the Kuskokwim River west of McGrath. In this bog, *C. rotundata*, growing in *Sphagnum balticum* was found within 30 yards of a large mixed stand of *C. aquatilis* and *C. rostrata*. (A map of this area is shown in *Contributions from the Gray Herbarium* in press.) Number *3271* is *C. rotundata*, and *3263* and *3265* are of the intermediate variable population. Some of these plants are very close to *C. rostrata* and grow on the edge of the patch of that species (on a silt bottom with floating *Sphagnum Lindbergii*). Other plants of these collections have an index even higher than any of the *C. paludivagans* population, indicating that they are closer to *C. rotundata*. This seems to be a mixture of (a) F_1 (3265), (b) back-crosses to the *C. rostrata* parent (3263-B) and (c) a second back-cross to *C. rostrata* (3263-A) (Compare the perigynia as shown in Fig. 2).

The whole of the *C. rostrata* population of the valley has been affected by introgression or gene flow. For example, on the margins of some of the bog-filled lakes, there are persistent zones of what in the field look like *C. rostrata* because of the contrast with the sedges in the center. However, when collections of these are analysed their character indices show that they are intermediates. For example, *C. paludivagans 4513* and *4516* were collected in the damp center of a bog in a clogged beaded drainage on the high terrace 70 miles upstream from McGrath. On the margin of this *4512* was collected as *C. rostrata* ("not quite typical"). Index analysis shows it to be of value 16 as if it were the result of an F_1 hybrid back-crossed to *C. rostrata*. These plants would casually be identified as *C. rostrata* although they show several intermediate characteristics.

In contrast to this, my collections show little evidence of repeated backcrossing to *C. rotundata*. This may be because of inadequate collections or the variability of the plants included in *C. rotundata* may indicate that such backcrossing has actually taken place. Alternatively, this may be an expression simply of a variable parental population. Without further evidence all plants with an index over 50 have been assigned to *C. rotundata.*

Probably for the same reason, all those specimens with an index less than 15 should be referred to *C. rostrata*, but I have not done so because of the complication with *C. rhynchophysa* discussed below. In the main area of the flats, *C. rostrata* occupies a relatively restricted habitat on the silt shores and *C. paludivagans* the mixed or transitional habitat. It is interesting to note that far down stream many miles from the flats area, and in the Kuskokwim Mountains, collection *1667* of *C. rostrata* (index 5) was found in a mixed bog habitat considered typical for *C. paludivagans.* Perhaps this is an example of colonization of a marginal habitat by *C. rostrata* where competition is lacking, while near McGrath *C. rostrata* is eliminated from such a habitat by *C. paludivagans.* Alternatively, it could be that genes for such a physiological variant which exist within the parental population find expression only when in an isolated patch removed from the main population. If so, the structural features are little modified correlated with the physiological. That some of the population of mixed parentage does move down river is shown by collections *2169* and *2084.* These two were collected where the Kuskokwim flows through the Kuskokwim Mountains, farther down river than the main bog area. Their habitats are disturbed also. Number *2169* was collected on the silt shores of an oxbow lake which had been entirely invaded by bog vegetation, although there was still conspicuous growth of coarse sedge and horsetails (*Equisetum fluviatile*). Number *2084* was collected on a slack-water beach along the main river among common weeds mixed with plants usually associated with bogs: *Triglochin palustre*, *Scirpus microcarpus*, *Eriophorum Chamissonis*, *Eriophorum angustifolium*, *Juncus alpinus*, *Juncus arcticus*, *Juncus castaneus*, *Ranunculus repens*, *Rumex occidentalis*, and *Rorippa islandica.*

Two collections, *2084* and *3263a*, strongly resemble *Carex rhynchophysa* C. A. Meyer of Hultén (1941) (*C. laevirostris* of Blytt and Fries). A detailed examination and the circumstances of their growth make me doubt that they should be identified as this species, especially when there also appear to be hybrids between this (*C. rhynchophysa*) and *C. rostrata*, and between it and *C. rotundata* (*3263, 3265*). The characters of the collections which strongly resemble *C. rhynchophysa* lie within the range of variation included in crosses between *C. rotundata* and *C. rostrata* and it seems preferable to regard them as resegregations of the characters of the two parent species as would be expected from uncontrolled back-crossing (Fig. 1, 2).

The evidence of back-crossing indicates the fertility and vigor of the *C. paludivagans* population. Segregation of the combinations formed in this way and gene flow back into the parental and new populations will provide new combinations and vigorous variability in the new populations of all three. In Table 3, the values assigned in making the character index show this variability. The collections of the three species are uniform in the numbers given, *C. rotundata* 3 and 4, *C. paludivagans* mostly 2, and *C. rostrata* 0 and 1. In contrast, the recently made hybrid populations by their spread of numbers show their variability.

Carex paludivagans Drury, sp. nov.

Loosely caespitose perennial of mixed peat and mineral soil environments; stolons about 1 mm. thick and as much as one meter long, horizontal, pale yellow; roots fibrous, 1 to several dm. long; fruiting culms (40–)45–50(–60) cm. tall, bluntly triangular, smooth or sparsely scabrous above, especially in the inflorescence, phyllopodic; culm bases coarse and soft, clothed with conspicuous shreds of previous years leaves; leaf-bases light brown or barely light-reddish-tinged in new sprouts; well-developed leaves 2, 3, or 4 to a fertile culm, below the middle (20–)30–40(–55) cm. long by 1–2.5 mm. wide, folded, obscurely to conspicuously septate-nodulose, stiff, firm, light green, scabrous-roughened especially on the keel and margins toward the attenuate tip; leaf sheaths tight, yellowish-brown-tinged ventrally, the fused margins about 2 mm. broad, whitish or yellow-tinged, hyaline, the throat truncate, but often torn in life to a length of 4–9 mm., the ligule reduced, barely 1 mm. long. Inflorescence 5–17 cm. long; terminal spike staminate, 22–45 × 1.5–2.5 mm., often with 1–2 smaller ones at its base; staminate scales 3.5–5.5 mm. long, acutish, brown, with a tan hyaline margin, apex and midrib; anthers 2.5–2.7 mm. long; filaments about 4 mm. long; pistillate spikes usually 2, sometimes 1, lateral, sometimes the upper lateral ones gynaecandrous, 11–35 × 7–11 mm., oblong; bracts leaflike, 4–20 cm. long × 1.5–2 mm. wide, longest on lowest spike, divergent; the short sheath hyaline below with a purplish, truncate or slightly concave throat; pistillate scales 2.6–3.8 × 1.2–1.5 mm., acute or abruptly acuminate, purplish brown with a white hyaline apex and lighter midrib, containing one conspicuous nerve; perigynia (40–)60–80(–90) to a spike, longer than the scale, 4–4.5 × 1.5–2.4 mm., ascending to spreading, closely packed to rather loose, oval, ovate or obovate, pale yellow-brown, straw colored or light shining brown, reddish dark brown at the apex and on the beak, inflated membranous, puncticulate, strongly nerved, substipitate; beak 1–1.5 mm. long, bidentate, the teeth 0.1–0.2 mm. long, stiff, acute; achenes 1.3 × 1 mm., obovate, brown, puncticulate, trigonous with blunt angles, concave below, continuous with the persistent, bent style, substipitate, loosely enveloped in the perigynium; stigmas 3, 2–2.5 mm. long, dark.

Laxe caespitosa, perenne, paludicola; stolonibus ca. 1 mm. latis, ad 1 m. longis, flavis; culmis (40–)45–50(–60) cm. altis, glabris basi, sparse scabris supra, phyllopodicis; basis crassis, mollibus, vaginis investis, pallide brunneis, aut castaneis stolonibus juvenibus; foliis 2–*3*–4, inferne, (20–)30–40(–55) cm. × 1–2.5 mm., replicatis, haud aut conspicue septatis-nodulatis, rigidis, scabris carina et margine ad attenuato apice; vaginis stricte cinctis ore vaginae truncato, hyalino. Infloresccenta 5–17 cm. longa, spico terminale mascule, 22–45 × 1.5–2.5 mm., haud infrequens 1–2 addendo baso; squamis masculis 3.5–5.5 mm. longis, acutis, obovatis, stramineis, pallide margine, apice et nervo centralo; antheris 2.5–2.7 mm. longis; filamentis ca. 4 mm. longis; spicis feminis (1) 2, lateralis, superne lateralia per occasionem gynaecandra, 11–35 × 7–11 mm., oblongis; bracteis divergentibus, 4–20 cm. longis, 1.5–2 mm. latis; breve vagina hyalina ore truncato; squamis feminibus 2.6–3.8 × 1.2–1.5 mm., acutis aut abrupte acuminatis, purpureis, fuscis, hyalino apice et nervo centralo; perigyniis squama longioribus, (40–)60–80(–90) spico, 4–4.5 × 1.5–2.4 mm., ascendentibus aut squarrosis, laxe ad dense compactis, ovalibus, ovatis aut obovatis, straminibus aut pallide nitentibus brunneis, atropurpureis apice et rostrate, inflatis, membranaceis, puncticulatis, glabriis, conspicue nervosis, substipitatis; rostris 1–1.5 mm. longis, bidentatis; dentibus 0.1–0.2 mm. longis, acutis, rigidis; achaenis 1.3 × 1 mm., obovatis, fuscis, puncticulatis, trigonis, continentibus persistente style, laxe involvitis perigyniis; stigmatibus 3, 2–2.5 mm. longis, fuscis.

Soligenous bogs and bog-invaded ox-bow lakes of the Upper Kuskokwim River Region of Alaska. **ALASKA:** In drying area of *Sphagnum balticum* with *Polytrichum* colonizing drier spots in the larger pond at the head of a beaded drainage running east off the high terrace 40 miles upstream from McGrath, Latitude 62° 58′ N and Longitude 155° 09′ W., August 11, 1950, *W. H. Drury, Jr. 4513;* In wet area of *Sphagnum balticum* in the center of larger pond at the head of a beaded drainage running east off the high terrace 40 miles upstream from McGrath, Latitude 62° 58′ N and Longitude 155° 09′ W., August 11, 1950, *W. H. Drury Jr. 4516;* In *Sphagnum Ångströmii* and *S. balticum* in bog-invaded interdune area near the junction of Middle Fork with the Big River, Latitude 62° 57′ N. and Longitude 154° 52′ W., August 14, 1950, W. H. Drury, Jr. *4543* (TYPE in the Gray Herbarium); In *Sphagnum Lindbergii* between bog ridges on top of the middle terrace west of Appel Mountain along Takotna River, Latitude 63° 01′ N and Longitude 155° 36′ W., August 22, 1950, *W. H. Drury, Jr. 4659.* Specimens will be deposited in the United States National Herbarium, the National Museum of Canada, the Gray Herbarium, and the Riksmuseet at Stockholm, Sweden. This citation includes those specimens considered to belong to the species *C. paludivagans.* Recent hybrids between *C. rostrata* and *C. rotundata* are not part of the *C. paludivagans* population. They include numbers: *2084*, *2169*, *3263-A*, *3263-B*, *3265*, *4341*, and *4512*.

The Problem of the Name

There are three names published which might be applied to the new population described here or to hybrids between *C. rostrata* and *C. rotundata: Carex rhynchophysa* C. A. Meyer, *Carex laevirostris* Blytt and Fries, and *Carex hymenocarpa* Drej.

Carex rhynchophysa and *C. laevirostris* are synonymous. Plants which on morphological grounds agree with this taxon were collected in two places in the Upper Kuskokwim Region. Hultén (1942) reports the species from two other places in Alaska and Porsild (1951) reports it from the Nisutlin River in Yukon Territory. This material does not match the population I have named *C. paludivagans* and is considered to be entirely separate from it. The collection from the Upper Kuskokwim which best matches *C. rhynchophysa* (*laevirostris*) (Fig. 2, No. 3263-A) was taken from a very variable hybrid swarm (*C. rostrata* × *C. rotundata*) and was found with both parents in one small part of one bog. Plants intermediate between No. 3263-A and *C. rostrata* and between No. 3263-A and *C. rotundata* (No. 3265) were found in the same stand. My other collection which matches *C. rhynchophysa* (2084) was also made in a mixed stand but less complete collections were made. The evident hybrid nature of this population throws doubt on the presence of the *C. rhynchophysa* taxon in Alaska. More important as far as the present problem is concerned is that the variable population which matches *C. rhynchophysa* differs in being large and coarse in contrast to the slender and small *C. paludivagans* population. The variable population (3263-A, 3263-B, 3265) differs also by this variability itself from the uniform populations of both *C. paludivagans* and *C. rhynchophysa*.

Carex hymenocarpa Drej. was described from Greenland in *Revis. Crit. Caricum Bor. in Terris Danic.*, p. 58; 1841. It is illustrated in Flora Danica Fasc. XLVIII, tab. MMDCCCLIX and described on page 12 of that volume. It is a cross between *C. rostrata* and *Carex saxatilis* L. (which many continental authors consider conspecific with *C. rotundata* and *C. physocarpa* Presl.). In the Upper Kuskokwim *C. rotundata* always has three stigmas and trigonous achenes. *Carex saxatilis* has two stigmas and lenticular achenes. Polunin (1943) reports that he collected sterile material of the hybrid in southwest Greenland

and the illustration in Flora Danica shows a plant with undeveloped achenes and empty perigynia. The plants illustrated have strongly red-purple leaf bases, rather narrow, but unfolded leaves, which are coarser than those of *C. paludivagans.* There are 2 male and 3 female spikes, perigynia are indicated as broadly elliptical in the description, but as illustrated are narrowly elliptical, abruptly contracted into a very short beak; the lowest bract of the inflorescence is ascending and flat; the achene illustrated appears lenticular but there are 3 stigmas protruding from the mouth of the perigynium illustrated next to it. The plants illustrated closely resemble my *4341*, which is a local hybrid resynthesis differing in several respects from the general population of *C. paludivagans.* This number *4341* was originally identified as an aberrant *C. rostrata* rather than *C. paludivagans* and this difference in aspect agrees with that of the plants illustrated in *Flora Danica.* Individual collections from the variable populations of recent hybridization in the Upper Kuskokwim Region can be chosen to match the type specimens of the three names mentioned, but all are evidently of unstable genetic structure, and they do not match *C. paludivagans* in morphology or in uniformity. For these reasons all three names are rejected.

Other Hybridization Within the Vesicariae

In the Upper Kuskokwim River Region there has been hybridization between nearly all of the species of this section: *Carex rostrata* × *Carex membranacea* Hook. (*3819, 3820*) and *Carex membranacea* × *Carex rotundata* (3844) have been found in addition to the cases discussed already (Fig. 2). These hybrid stands were of local occurrence and were closely associated with their parents on unstable morainic deposits thinly covered by a shallow bog.

Hultén (1942) reports six specimens that he called hybrids of *C. physocarpa* Presl with *C. rostrata.* He gives them no name but points out that *C. saxatilis, C. physocarpa* and *C. rotundata* grade into each other in certain parts of their ranges.

Discussion

Although there can be no doubt of the importance of geographic isolation in the process of speciation, and of reproductive isolation as the ultimate criterion of species status in plants or animals, the lack of mobility of plants has resulted in the persistence of transitional evolutionary stages which require special consideration. In many animals complex behavior patterns have developed in response to the problems presented by mobility and consequent repeated overlap of populations. Plants are characteristically subject more to isolation than repeated approximation and complex isolation mechanisms in many cases do not seem to have developed. With the opening of glaciated regions of North America to colonization, the vegetation has been fundamentally disturbed and integrated populations brought into proximity that were previously isolated. Evident results of this are the swarms of variants found in *Salix, Betula, Quercus, Rubus,* and so on, the classification of which has led to dismal failures when based solely on morphological concepts. In these groups, integrated self-maintaining populations preserve their identity in the face of continued and widespread hybridization with neighboring populations.

Among plants, isolation can be on a small scale. Disturbance of conditions by man and a variety of other natural conditions has brought formerly spatially isolated populations together which lack genetic isolating mechanisms and have crossed freely. Plants are long-lived and a hybrid once formed has the opportunity of producing large numbers of sex cells thereby increasing the opportunity for recombination thus increasing the probability that a fertile type capable of perpetuating itself will arise.

Because of the ability of many groups of plants to maintain population integrity within a framework of and in the presence of broad interbreeding, many botanists can accept only degrees of breeding isolation as a criterion of species. Zoologists understandably and correctly consider two populations broadly interbreeding as one species and suggest that botanists do so too. Botanists, however, have found many clear species populations which do overlap broadly and intergrade. It is as if the enforced crossbreeding that can be brought about in captivity within the genus *Anas, Papilio,* or *Larus* can be and is brought about repeatedly and locally by disturbance of the site. Both are "artificial" but of a different type of artificiality. Many zoologists deny introgression, calling it gene flow within a species.

Given their definition, this is correct. But the botanists cannot accept this clear, logical, and simple definition because their experience with living material denies it. Experience with populations such as these of *Carex* can be repeated in *Salix* and several other genera of the North. In them consistent groupings of characteristics into integrated populations emerge from a spectrum of variation and interbreeding. They continue to exist in the presence of marginal interbreeding and deny biological reality to a consideration of the whole spectrum as one species. The genetical basis for the emergence of integrated populations or their preservation certainly is not clear, but must be presumed to involve balanced complexes of genes, which are selected as balanced wholes. When hybrids form, as they seem to freely, they are eventually selected against, but individuals persist for a long time. The only measure of their status in the population as a whole is their ability to spread away from the clearly hybrid zone.

In the general stream of evolution of plants, hybridization such as is considered in these species of *Carex* must have been an important force in creating genetic variability on the species level, especially in disturbed areas following glaciation or man's influence. I do not see, however, that Anderson and Stebbins (1954) have established how any really new genetic material can be created out of recombinations. Introgression must remain a detail and one of many mechanisms of change.

Summary

The transition of habitat from silt-shored sweet-water oxbow lakes to water saturated with organic matter in peat bogs is very widespread in the Upper Kuskokwim River Region and in this transition, a hybrid population of *Carex* has become established. The hybrid population is forming continually and backcrossing to the parents occurs, most conspicuously to *C. rostrata* as indicated by my collections. But, in addition to the variable hybrid swarms present in several bogs, there is a uniform and fertile population which has been segregated and selected out and expanded, that is becoming more abundant and widespread than both parents. This population exhibits little of the variability characteristic of a hybrid swarm and seems to maintain clear genetic integrity without becoming swamped

with gene flow between it and its parents. On the basis of its existence as a discrete, homogeneous, fertile population maintaining its identity, I am convinced that this constitutes a species. Perhaps most important of all it shows clearly the sort of populations found among plants in the field which lead many botanists to conclude that there is no complete agreement with zoologists on details of delimitation of species and the means of their formation. Conditions such as the ones under discussion would be nearly impossible among the higher animals. It may well be that in this population of *Carex* allopolyploidy or some aneuploidy will explain the jump isolation. Cytological studies would decide this, but attempts to germinate seed were unsuccessful.—BIOLOGICAL LABORATORIES, HARVARD UNIVERSITY.

Literature Cited

Anderson, E. 1949. Introgressive Hybridization. John Wiley and Sons, New York.

Anderson, E. and L. Hubricht. 1938. Hybridization in Tradescantia III. The Evidence for Introgressive Hybridization. Am. Journ. Bot. **25**: 396–402.

Anderson, E. and G. L. Stebbins. 1954. Hybridization as an Evolutionary Mechanism. Evolution **8**: 378–388.

Hultén, E. 1942. Flora of Alaska and Yukon. Lunds Univ. Arssk. N. F. Avd. 2. **38**: 378–383.

Polunin, N. 1943. Contributions to the Flora and Phytogeography of Southwestern Greenland: an enumeration of the vascular plants with critical notes. Journ. Linn. Soc. London **52**: 375.

Sibley, C. 1954. Hybridization in the Red-eyed Towhees of Mexico. Evolution **8**: 252–290.

Availability of Ingredients for Plastic.—In describing the Archer Method for Mounting Herbarium Specimens (Rhodora **57**: 294–299. 1955), I mentioned that Ethocel and Dow Resin were available only in relatively large containers. This statement was based on information supplied two years ago by the Dow Chemical Company. Dr. John R. Reeder called my attention to the fact that this company is now prepared to supply Ethocel and Dow Resin in smaller quantities. Readers might be interested in a recent communication from Dow Chemical Company in which Dow Resin 276-V2 is offered for sale in small quantities at the rate of thirty-two and a half cents per pound, f.o.b. Midland, Michigan. Similarly, Ethocel is quoted at eighty-one or eighty-six cents per pound depending upon the viscosity rating.—Reed C. Rollins, GRAY HERBARIUM.