



# Botanical Notes

A newsletter dedicated to dispersing taxonomic and ecological information useful for plant identification and conservation in Maine

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## IDENTIFICATION AND TAXONOMY OF TWO DIFFICULT MARITIME HYBRIDS WITH *CAREX PALEACEA*

Members of *Carex* section *Phacocystis* are well known for taxonomic difficulties created by interspecific hybridization. This situation appears to be pronounced in coastal and estuarine areas of northeastern North America (Lepage 1956, Cayouette and Morisset 1985). Careful research has revealed a complex evolutionary history in this section (Cayouette and Morisset 1985, Standley 1990). Cayouette (1987) has shown that misapplication of *Phacocystis* names has occurred in the northeast due to hybrid-derived taxa simulating the morphology of other species. The name *C. salina* Wahlenb. has commonly been applied to a set of rare plants from coastal Maine (Fernald 1950, Gleason and Cronquist 1991). These individuals are now known to consist of two, stabilized hybrid derivatives—*C. recta* Boott and *C. vacillans* Drejer ex Hartman. This note seeks to clarify the taxonomy of the two stabilized hybrid species and present their identifying characteristics.

*Carex* section *Phacocystis* (including sections *Acutae* and *Cryptocarpae*) contains primarily perennial, wetland species of small to moderate stature. This section belongs to subgenus *Carex*, as evidenced by its mostly unisexual spikes and entire or equally bifid beaks (Standley 1985). It is somewhat unusual, however, in that it possesses bicarpellate gynoecia (*i.e.*, two carpels per flower), a trait usually associated with

subgenus *Vignea*. Members of section *Phacocystis* were formally divided into two separate sections—*Acutae* and *Cryptocarpae*. The former section was generally identified by upright, sessile spikes, non-indented achenes, and awnless carpellate scales, while the latter section was identified by drooping, peduncled spikes, commonly indented achenes, and carpellate scales with long awns. Species with intermediate morphology do occur. The discrepant placement of *Carex torta* Tuckerman—a species with arching, shortly-peduncled lower spikes and awnless carpellate scales—by Fernald (1950) and Gleason and Cronquist (1991) illustrates the difficulty of drawing section boundaries. Based on intermediate taxa and the shared character state of bicarpellate gynoecia, these two sections are now considered to comprise one, variable section (*Phacocystis*) (Standley 1985).

### DESCRIPTION OF THE PARENTAL SPECIES

Following is a brief discussion of the three parental species. Descriptions of the ecology and morphology is provided, with focus on characters that allow for discrimination of the stabilized hybrid taxa.

*Carex paleacea* Wahlenb. inhabits coastal salt marshes of north temperate to arctic regions of eastern North America. In Maine, it is commonly found in association with *Juncus gerardii* Loisel., *Schoenoplectus pungens*, and *Triglochin maritimum* L. Its flowering stems share morphological similarity with *C. crinita* Lam. (*i.e.*, spikes borne on drooping peduncles and carpellate scales with conspicuous,

scabrous awns) (Figure 1). *Carex paleacea* differs from its inland counterpart, however, in its possession of long rhizomes and lack of cespitose growth form. This maritime species has yellow-brown carpellate scales and short-papillose perigynia with 0-5 obscure nerves on each face. The inflorescence is overtopped by a long, bract that subtends the lowest spike. The achenes of *C. paleacea* normally have an evident indentation on one side (Figure 2).



Figure 1. Inflorescence of *Carex paleacea*.

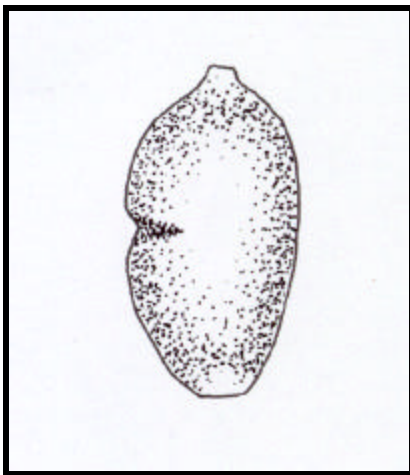


Figure 2. Illustration of *Carex paleacea* achene. Note indentation on left side.

*Carex nigra* (L.) Reichard is usually found growing in open, sometimes disturbed, habitats near the Atlantic coast. This includes meadows, lawns, and roadsides of coastal towns and provinces. *Carex nigra* possesses an inflorescence with sessile, erect spikes that are usually not overtopped by the lowest bract (Figure 3). The carpellate scales are dark purple-brown with a very narrow, pale midvein. The perigynia usually bear several conspicuous nerves on each surface and are densely long-papillose. The beak frequently has minute scabrulæ around the orifice (Figure 4).



Figure 3. Inflorescence of *Carex nigra*.



Figure 4. *Carex nigra* perigynium, apical portion. The arrow points to scabrulæ about the orifice of the beak. Note also the long papillae on the perigynium surface.

*Carex aquatilis* Wahlenb. is a polymorphic, circumboreal species. In Maine, it normally inhabits open, freshwater wetlands with moderate to high mineral soil content (*i.e.*, it is only infrequently found in peatlands). This species is essentially non-maritime, however, it plays a role in *Phacocystis* speciation with maritime species. *Carex aquatilis*, similar to *C. nigra*, possesses sessile, erect spikes. However, *C. aquatilis* has a very long, primary bract that exceeds the height of the inflorescence (Figure 5). It has red-brown to purple-brown carpellate scales with a narrow midvein and nerveless or inconspicuously nerved perigynia that lack prominent papillae on the surface. The orifice of the beak is entire and lacks scabrulæ (Figure 6).



Figure 5. Inflorescence of *Carex aquatilis*. Note the very long lowest bract of the inflorescence (bent to the right) that, when straightened, would exceed the total height of the inflorescence.



Figure 6. *Carex aquatilis* perigynium, apical portion. Note the lack of scabrules around the beak orifice and absence of long papillae on perigynium surface.

#### DESCRIPTION OF THE PROBLEM

*Carex* section *Phacocystis* includes both estuarine and palustrine species. The species are brought into contact both spatially and phenologically in the coastal Maine region. The proximity of fresh and brackish water habitats coupled with shortened growing season of higher latitudes is believed to contribute to the extensive hybridization seen in this section. Furthermore, storm and ice disturbances of this region may contribute to bringing species together and creating new habitats for hybrid plants (Standley 1990). Most reported *Phacocystis* hybrids are short-lived first-generation hybrids with reduced fertility (Standley 1990). Several hybrid taxa, however, appear to be wide-spread and persistent, including *C. recta* and *C. vacillans*. These two species demonstrate lower fertility than their diploid progenitors, however, they are capable of producing viable seeds and appear to successfully utilize vegetative reproduction (Standley 1990).

The name *Carex salina*, which has been incorrectly applied to Maine plants, has been shown to be the stabilized hybrid derivative of *C. paleacea* and *C. subspathacea* (Standley 1990). Evidence substantiating this theory came from many sources, including morphology, anatomy, allozymes, and chromosomal behavior. *Carex salina* occurs in Canada and Eurasia, but is not a member of the United States flora. Plants formally referred to as *C. salina* from Maine need to be identified as one of two species—*Carex recta* or *C. vacillans*. These two species are similar to *C. salina* in that they are stabilized hybrids that demonstrate slightly disturbed meiotic pairing and lower pollen stainability than parental species (such as *C. paleacea*) (Cayouette and Morisset 1985). *Carex recta* is known to be the hybrid derivative of *C. aquatilis* and *C. paleacea*, while *C. vacillans* is the hybrid derivative of *C. nigra* and *C. paleacea*. Figure 7 graphically summarizes the relationship of the involved species.

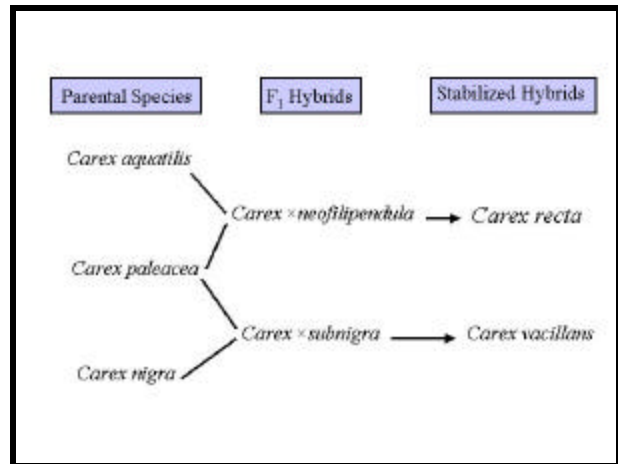


Figure 7. Reticulogram showing relationship of *Carex aquatilis*, *C. xneofilipendula*, *C. nigra*, *C. paleacea*, *C. recta*, *Carex xsubnigra*, and *C. vacillans*. First generation hybrids (F<sub>1</sub>) are discussed later in the text.

As *C. recta* and *C. vacillans* share a common parent (*C. paleacea*) they are morphologically similar and difficult to distinguish without careful study. Both species possess similarity in form, including ascending to spreading lower spikes borne on short peduncles (mostly 0.6–2.0 cm long) (Figure 8). They have acuminate-pointed to shortly-awned carpellate scales. Though producing rhizomes, *C. recta* and *C. vacillans* sometimes have a subcespitose growth form, particularly when substrate is limited (*i.e.*, growing in cracks of rock). Additionally, they normally possess an elongate lowest bract that overtops the uppermost spike of the inflorescence. Separation of *C. recta* and *C. vacillans* requires detailed examination of floral scales, perigynia, and achenes. Table 1 provides comparative

morphological information for maritime *Phacocystis* of Maine. Synonyms are located at the end of the article.



Figure 8. *Carex recta*. General form of both *C. recta* and *C. vacillans*. Note the spreading lower spike.

#### DESCRIPTION OF THE STABILIZED HYBRIDS

The term stabilized hybrid means that a taxon has been shown to be of hybrid origin, but behaves as a species. Traits often associated with stabilized hybrids include: relatively uniform morphology; novel character states not seen in first generation hybrids; ability to produce some viable fruit; and/or reasonably widespread distribution that includes occurrences where one or both parental species are not present. *Carex recta* and *C. vacillans* meet well the description of stabilized hybrids.

*Carex recta* and *C. vacillans* occur in coastal habitats. This includes tidal marshes, crevices in beach outcrops, and open meadows of small islands. They are rarely, if ever, sympatric with both parents in Maine (Haines, personal observation). Both species are ranked S1 by the Maine Natural Areas Program (1999).

*Carex recta* is the stabilized hybrid derivative of *C. aquatilis* and *C. paleacea*. It, therefore, is relatively intermediate in the morphology of its parental progenitors. Its carpellate scales are normally bronze to brown with a relatively wide central band that occupies 33–50 percent of the total scale width (Figure 9). The wide midrib is prolonged and always reaches the apex of the scale. *Carex recta* possesses obscurely nerved perigynia that are short-papillose and lack scabrules around the orifice of the beak (Figure 10). Its achenes, observed by removing them from the perigynia, are generally lustrous and folded on one surface (Figure 11). Observations of achene luster and shape must be made on well-formed seeds. As *C. recta* may show a high proportion of malformed and infertile achenes, care must be taken to locate mature material.



Figure 9. Carpellate scale of *Carex recta* showing relatively wide midvein.



Figure 10. Perigynium of *Carex recta*. Note the absence of several prominent nerves.

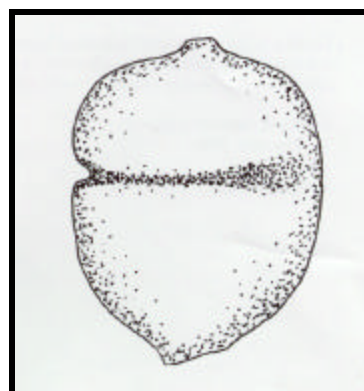


Figure 11. Illustration of *Carex recta* achene. Note fold across surface.

*Carex vacillans* is the stabilized hybrid derivative of *C. nigra* and *C. paleacea*. Though generally similar to *C. recta*, the different parental combination has provided several subtle clues to its identity. The carpellate scales are usually dark brown to purple-brown and have a narrow midrib occupying 10–33 percent of the total scale width (Figure 12). In some collections, the midrib is evanescent and does not reach the apex of the scale. The perigynium of *C. vacillans* usually possesses 2–5 nerves of each face, is densely long-papillose, and often will possess a few scabrules around the orifice of the beak (Figure 13). The achenes are generally dull and lack a constriction.



Figure 12. Carpellate scale of *Carex vacillans* showing relatively narrow midvein.



Figure 13. Perigynium of *Carex vacillans*. Note the several raised nerves.

Species	Primary Bract	Lowest Spike	Carpellate Scales	Perigynium Surface	Achenes
<i>C. nigra</i>	shorter than to subequal to inflorescence	erect and sessile	dark purple -brown, without awns	densely long-papillose, 3–9 nerves on each surface	white-iridescent, not indented
<i>C. paleacea</i>	longer than inflorescence (rarely equal to)	drooping on long peduncles up to 7.5 cm long	yellow-brown, with scabrous awns to 1 cm	short-papillose, 0–5 obscure nerves on each surface	lustrous, indented on one side
<i>C. recta</i>	longer than inflorescence (rarely equal to)	ascending to spreading on peduncles 0.6–2.0 cm long	bronze to brown, pointed or with short awns	short-papillose, obscurely nerved	lustrous, folded on one face
<i>C. vacillans</i>	longer than inflorescence (rarely equal to)	ascending to spreading on peduncles 0.6–2.0 cm long	dark brown to purple-brown, pointed or with short awns	long-papillose, 2–5 nerves on each surface	dull, not indented

Table 1. Comparison of key morphological features of maritime *Phacocystis* in Maine.

Table 1 presents a somewhat simplified view of the maritime *Phacocystis* morphologies likely to be encountered in Maine. Complicating identification is the fact that the stabilized hybrids do cross with the other coastal progenitor species (*C. nigra* and *C. paleacea*) to create an extremely complicated situation. The reader is referred to Cayouette and Morrisett (1985) for detailed morphological comparisons of many hybrid combinations.

#### FIRST GENERATION HYBRIDS

It is important to note that the process that created *Carex recta* and *C. vacillans* (interspecific hybridization between respective *Phacocystis* species) is an ongoing phenomenon. Therefore, the progenitor species continue to produce the first generation hybrids that gave rise to the stabilized hybrids. The first

generation hybrids are very similar to the stabilized hybrids and likewise display morphological intermediacy, reduced fertility, and chromosomal abnormalities (*e.g.*, disturbed meiotic pairing). However, the stabilized hybrids (*C. recta* and *C. vacillans*) do not demonstrate the severity of chromosomal abnormalities or infertility as do the first generation hybrids. Furthermore, Cayouette and Morrisett (1985) have shown that the stabilized hybrids are not perfectly intermediate in morphology between their parental progenitor species. Rather, they show one or more subtle, novel character states. For example, as previously noted, the achenes of *C. aquatilis* are not indented on one side whereas those of *C. paleacea* are. Therefore, the hybrid (called *C. ×neofilipendula*) would be expected to show, and commonly does, a slight indentation on one side of the achene. However, *C. recta*, the stabilized hybrid of

these two species, possesses a transverse fold across one surface of the achene. This character state is not seen in either parent. Discriminating between first generation hybrids and stabilized hybrids by morphology alone is extraordinarily difficult without intimate familiarity with these species. Recent trend has been to consider first generation hybrids and stabilized hybrids by the same name (Bruederle, Cayouette, and Standley, in ed.). The first generation hybrids, identified by the “×” symbol, and their parental composition are provided in the following list of synonyms.

#### IMPORTANT SYNONYMS

##### *Carex recta*

- C. kattegatensis* Fries ex Lindmann
- C. salina* Wahl. var. *kattegatensis* (Fries ex Lindman) Almquist in Hartman
- C. ×neofilipendula* Lepage (*C. aquatilis* × *C. paleacea*)

##### *Carex vacillans*

- C. ×subnigra* Lepage (*C. nigra* × *C. paleacea*)
- C. ×super-goodenoughii* (Kükenth.) Lepage (*C. nigra* × *C. recta*)

#### Literature Cited

Bruederle, L., J. Cayouette, and L.A. Standley. in ed. *Carex* section *Phacocystis* Dumort. in *Flora of North America* Editorial Committee. *Flora of North America*. Oxford University Press, NY.

Cayouette, J. 1987. *Carex lyngbyei* excluded from the flora of eastern North America, and taxonomic notes on related species and hybrids. *Canadian Journal of Botany* 65: 1187–1198.

Cayouette, J. and P. Morisset. 1985. Chromosomal studies on natural hybrids between maritime species of *Carex* (sections *Phacocystis* and *Cryptocarpae*) in northeastern North America, and their taxonomic implications. *Canadian Journal of Botany* 63: 1957–1982.

Fernald, M.L. 1950. *Gray's Manual of Botany*, eighth edition. Van Nostrand Reinhold Company, New York, NY.

Gleason, H.A. and A.C. Cronquist. 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, second edition. The New York Botanical Society, Bronx, NY.

Leepage, E. 1956. Études sur quelques plantes américaines. IV. *Carex*-hybrides. *Naturaliste Canad.* 83: 105–156.

Maine Natural Areas Program. 1999. *Elements of Natural Diversity: Rare, Threatened, and Endangered Plants*. Department of Conservation, Augusta, ME.

Standley, L.A. 1985. Systematics of the *Acutae* group of *Carex* (Cyperaceae) in the Pacific northwest. *Systematic Botany Monographs*, volume 7.

\_\_\_\_\_. 1990. Allozyme evidence for the hybrid origin of the maritime species *Carex salina* and *Carex recta* (Cyperaceae) in eastern North America. *Systematic Botany* 15(2): 182–191.

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