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Foliar micro-morphology of *Carex* sect. *Phacocystis* in northern Europe

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A micro-morphological analysis of leaf epidermis (adaxial and abaxial sides) of fifteen taxa of *Carex* section *Phacocystis* was carried out using light microscopy and scanning electron microscopy (SEM). Three taxa were epistomatic (*C. nigra* var. *nigra*, *C.nigra* var. *juncea* and *C. subspathacea*), seven taxa were hypostomatic (*C. acuta*, *C. bigelowii* ssp. *bigelowii*, *C. bigelowii* ssp. *rigida*, *C. cespitosa*, *C. elata*, *C. lyngbyei* and *C. paleacea*) and five amphistomatic (*C. aquatilis*, *C.* × *halophila*, *C. rufina*, *C. stans* and *C. trinervis*). Epidermal modifications such as prickles were present in many species. The micro-morphological leaf characters of the investigated species were found to be important for distinguishing individual taxa but not for subsectional classification.

Leaf characters are preceded only by flowers and fruits in their use and value in taxonomic studies (Stace 1984). They are particularly valuable taxonomic features because they are generally present on the plant for a much greater part of its lifespan than the reproductive organs. According to Reznicek and Catling (1986), leaves have been underused for taxonomic studies in *Carex*. The main reason for this could be that at first sight the linear leaves of *Carex* may not look very promising as a taxonomic tool. The foliage leaves are generally separated into a sheath and a linear dorsi-ventral blade with a ligule at the apex of the sheath. The macro-morphological features seem to show limited variation. However, microscopic studies reveal many variable characters that include size, shape, orientation and anti-clinal wall undulation of epidermal cells (Stace 1984). Modifications of epidermal cells like papillae, silica bodies, prickles and stomata, plus the position, shape, size and distribution of these modifications can be of diagnostic value in plant taxonomy (Metcalfe 1971, Prychid et al. 2004). Some of these features have been revealed through leaf anatomical studies of *Carex* (Hjelmqvist and Nyholm 1947, Jalas and Hirvelä 1964, Metcalfe 1971, Standley 1987).

Micro-morphological characters have been used either on their own (Dean and Ashton 2008) or in combination with other data such as cytology (Standley 1987). Both quantitative (Standley 1986, Dean and Ashton 2008) and qualitative approaches (Standley 1985) show leaf surface micro-structure as an important tool in classifying closely related species in the genus *Carex*, for example Standley (1987) found differences in leaf epidermal characters among species of section *Phacocystis* from North America.

Identification of the species in section *Phacocystis* is frequently problematic because of limited variation and overlapping characters between species due to hybridisation. In this study, we use scanning electron microscopy (SEM) to examine the adaxial and abaxial leaf surfaces of twelve species (and several subspecies or varieties and hybrids) in *Carex* sect. *Phacocystis*. The purpose was to assess the taxonomic utility of the micro-morphologic characters in section *Phacocystis* from northern Europe. In order to identify homologous micro-morphological characters, we compare the results to Nakamatte and Lye (2007), where AFLP was used to show the genetic relationships of the species.

Material and methods

Plant material

Investigated plants are herbarium specimens of the species in section *Phacocystis*, available at Oslo (O) and UMB (NLH) herbaria; the collections are from a large part of northern Europe (Table 1). For most species, leaves from 5–10 populations were photographed by SEM, but many more collections were studied using a binocular microscope. For this study, emphasis was on plants (35 populations) that had previously been subjected to genetic differentiation analysis using AFLP (Nakamatte and Lye 2007, unpubl.), though other plants were also added. *Carex lyngbyei* is

Table 1. Plants used for SEM photography. Plants used for AFLP analysis (Nakamatte and Lye 2007, unpubl.) have collection numbers given in bold types. Vouchers in herbarium (O).

Species	Pop.	Country	Region	Locality	Coordinates	Altitude (m a.s.l.)	Collector	Number
C. acuta	202	Norway	Vestfold	Lardal, Lågen	09°59′25″E, 59°25′26″N	38	Lye	28467
C. acuta	241	Norway	Nord-Trøndelag	Steinkjær, Snåsavatn	11°34′E, 64°06′N	22	Lye	28513
C. acuta	300	Norway	Oppland	Ringebu, south of Elstad	10°10′20″E, 61°29′54″N	183	Lye	28574
C. acuta	387	Sweden	Ångermanland.	Nordmaling, south of Olofsfors	19°26′40″E, 63°34′21″N	0.3	Nakamatte	28690
C. acuta	391	Finland	Ostrobottnia boreal	southwest of Tervola	24°45′E, 66°03′N	40	Nakamatte	28694
C. acuta	656	Norway	Akershus	Ås, Årungen, south end	10°44′45E, 59°40′37″N	34	Nakamatte	29869
C. aquatilis	157	Norway	Troms	Tromsø, north of Prestvatn	18°56′28″E, 69°39′37″N	96	Lye	28412
C. aquatilis	382	Norway	Telemark	Tinn, Mæl, near Måna	08°47′E, 59°55′N	192	Lye	28685
C. aquatilis	389	Sweden	Nordbotten	1 km east of Kalix	23°12′E, 65°49′N	0.1	Nakamatte	28692
C. aquatilis	1024	Finland	Lapponia	Enontekio town	23°36′29″E, 68°23′13″N	290	Lye	30730
C. aquatilis	1026	Finland	Lapponia	west of Enontekio	23°32′37″E, 68°22′44″N	290	Lye	30732
C. bigelowii ssp. *bigelowii*	255	Norway	Nordland	Fauske, Sulitjelma	16°05′E, 67°07′N	180	Lye	28527
C. bigelowii ssp. *bigelowii*		Canada	Quebec	River Nastapoka	76°24′35″W, 56°52°55′ N	200	Roy et al.	C 460-83
C. bigelowii ssp. *bigelowii*		Canada	Quebec	Fort Chimo area	68°18′W, 58°07′N		Calder	2217
C. bigelowii ssp. *bigelowii*		Canada	Quebec	Baffin Island, South Igaluit	68°30′W, 63°45′N		Elven	3571/99
C. bigelowii ssp. *bigelowii*	750	Canada	Quebec	Labrador, Blanc-Sablon	57°09′W, 51°25′N	80	Lye	30053
C. bigelowii ssp. *rigida*		Norway	Vest-Agder	Sirdal, Austmannaskardet	06°59′05″E, 59°01′10″N	930	Lye	16860
C. bigelowii ssp. *rigida*	250	Norway	Nordland	Rana, Polar Circle	15°19′17″E, 66°33′07″N	670	Lye	28522
C. bigelowii ssp. *rigida*	321	Norway	Hedmark	Alvdal, Tronden	10°42′E, 62°10′N	1290	Nakamatte	28611
C. bigelowii ssp. *rigida*	333	Norway	Oppland	Dovre, Grimsdalen	09°40′E, 62°05′N	850	Lye	28628
C. bigelowii ssp. *rigida*	521	Norway	Oppland	Ringebu, Segalstadsæterkampen	10°07′50.5″E, 61°27′34″N	1050	Lye	29128
C. cespitosa		Denmark	Jylland, Århus amt	Åmølle southwest of Hadsund	10°06′10″E, 56°41′18.5″N	2	Lye	20177
C. cespitosa	66	Norway	Akershus	Ås, south of Pollevatn	10°44′36″E, 59°44′12″N	1	Nakamatte	27961
C. cespitosa	390	Finland	Ostrobottnia boreal	southwest of Tervola	24°45′E, 66°03′N	40	Nakamatte	28693
C. cespitosa	414	Norway	Finnmark	Kautokeino, Gukkesjavri	22°41′52″E, 69°18′29″N	390	Nakamatte	28721
C. cespitosa	683	Norway	Troms	Skånland, Tennvatnet	16°40′55″E, 68°30′59″N	25	Lye	29912
C. elata		Norway	Buskerud	Ringerike, Lamyra-Storelv	10°14′58″E, 60°07′08″N	82	Lye	18240
C. elata		Denmark	Jylland, Århus amt	Åmølle southwest of Hadsund	10°06′10″E, 56°41′18.5″N	2	Lye	20179
C. elata	73	Norway	Akershus	Aurskog-Høland, Røytjern	11°37′11″E, 59°52′28″N	227	Lye	27992
C. elata	107	Norway	Akershus	Asker, Semsvatn	10°25′50″E, 59°51′38″N	145	Nakamatte	28354
C. elata	564	Sweden	Närke	Karlskoga, Villingsberg	14°42′50″E, 59°17′38″N	150	Lye	29215
C. elata ssp. *omskiana*	560B	Finland	Karelia australis	8 km northwest of Taavetti	27°42′28″E, 60°56′45″N	75	Lye	29211
C. lyngbyei	906	Iceland	southwest Iceland	Reykjavik, Bakkatjörn	22°01′01″W, 64°09′26.6″N	3	Lye	30603
C. lyngbyei	927	Iceland	north Iceland	Miđfjördur, below Laugarbakki	20°54′58.5″W, 65°19′19″N	0.5	Lye	30625
C. lyngbyei	940	Iceland	north Iceland	Mývatn, Garđur	17°03′06.5″W, 65°34′16″N	280	Lye	30640
C. lyngbyei	963	Iceland	south Iceland	Kirkjubæjarklaustur, Efrivik	17°57′12.3″W, 63°46′34″N	10	Lye	30663
C. lyngbyei	970	Iceland	Southwest Iceland	100 m west of Stokkseyri	21°04′36″W, 63°50′29.2″N	4	Lye	30670
C. nigra var. *juncea*	252	Norway	Nordland	Saltdal, Junkerdal	15°34′E, 66°47′N	210	Lye	28524
C. nigra var. *juncea*	297	Norway	Oppland	Ringebu, south of Elstad	10°10′20″E, 61°29′54″N	183	Lye	28572
C. nigra var. *juncea*	384	Sweden	Värmland	Årjäng, Sanda	12°16′E, 59°22′N	137	Nakamatte	28687
C. nigra var. *juncea*	402	Norway	Finnmark	Sør-Varanger, Svanvik	30°05′E, 69°30′N	23	Nakamatte	28706
C. nigra var. *juncea*	673	Norway	Troms	Tromsø, Rudvang	18°43′49″E, 69°38′24″N	0.1	Lye	29896
C. nigra var. *juncea*		Norway	Østfold	Hobøl, south of Hobøl church	10°55′13″E, 59°35′50″N	95	Lye	30853
C. nigra var. *nigra*	84	Norway	Østfold	Hvaler, Asmaløy	10°57′E, 59°02′N	5	Lye	28322
C. nigra var. *nigra*	376	Norway	Rogaland	Gjesdal, Hunnedalen	06°36′E, 58°53′N	640	Lye	28679
C. nigra var. *nigra*	483	Scotland	Highlands	Loch Flut	04°05′E, 57°57′N	0.2	Lye	28988
C. nigra var. *nigra*	734	Canada	Newfoundland	Avalon Peninsula, S. Dildo	57°31′W, 53°33′N	1	Lye	30036
C. nigra var. *nigra*	1027	Norway	Troms	Tromsø, Tromsdalen	19°03′40.5″E, 69°36′17″N	465	Lye	30733
C. nigra var. *nigra*	1029	Norway	Troms	Tromsø, Tromsdalen	19°02′46″E, 69°35′56″N	510	Lye	30735

Table 1 (*Continued*)

Species	Pop.	Country	Region	Locality	Coordinates	Altitude (m a.s.l.)	Collector	Number
C. nigra var. *nigra*		Norway	Akershus	Ås, Kinn	10°45′21″E, 59°40′48″N	50	Nakamatte	31329
C. paleacea	78	Norway	Oslo	Malmøya, Solvik	10°45′E, 59°52′N	0.1	Nakamatte	28312
C. paleacea	240	Norway	Sør-Trøndelag	Skaun, west of Buvika	10°07′E, 63°19′N	0.3	Lye	28512
C. paleacea	287	Norway	Nord-Trøndelag	Nærøy, Bogan	12°12′E, 64°56′N	0.2	Lye	28560
C. paleacea	759	Canada	Labrador	Mary's Harbour	55°49′53″W, 52°18′45″N	0.2	Lye	30062
C. paleacea		Norway	Akershus	Frogn, Botn (Bunnefjorden)	10°42′47″E, 59°42′60″N	0.1	Nakamatte	31330
C. rufina	335	Norway	Møre and Romsdal	Stranda, Geiranger	07°17′E, 62°02′N	1030	Lye	17201
C. rufina	377	Norway	Vest-Agder	Sirdal, Austmannaskardet	06°59′05″E, 59°01′10″N	920	Lye	28680
C. rufina	687	Norway	Nordland	Narvik, Gátternjunni	18°05′E, 68°25′N	850	Lye	29917
C. rufina	569B	Norway	Rogaland	Suldal, west of Sandvatnet	07°02′17″E, 59°39′25″N	970	Lye	29222
C. rufina	576	Norway	Rogaland	Forsand, north of Akslaråtjønna	06°38′48″E, 59°01′08.5″N	950	Lye	29231
C. rufina	946	Iceland	East Iceland	Fjarđarheiđi, River þverá	14°14′22.5″W, 65°15′41″N	600	Lye	30646
C. stans	878	Greenland	Qeqertarsuaq	Disko Island, Blæsedalen	53°28′W, 69°19′N	3	Westergaard	30084
C. stans	4634	Greenland	North Greenland	Thule, Dundas Bay	68°45′W, 76°33′N		Westergaard	4634
C. subspathacea		Norway	Troms	Nordreisa, Leirbukta, Solstad	20°58′31″E, 69°46′30″N	0.1	Lye	12814
C. subspathacea	160	Norway	Troms	Tromsø, Museumstranda	18°54′11″E, 69°38′07″N	0.1	Lye	28415
C. subspathacea	172	Norway	Troms	Karlsøy, Skogsfjord	19°05′35″E, 70°01′04″N	0.1	Lye	28429
C. subspathacea	915	Iceland	west Iceland	Borgarnes, below Borg church	21°54′50″W, 64°33′25.5″N	0.1	Lye	30612
C. subspathacea	977	Iceland	southwest Iceland	sea-shore below Mosfellsbær	21°41′59″W, 64°10′36.4″N	0.2	Lye	30677
C. trinervis		Denmark	Øst-Jylland	Riebe, Rømø	08°28–30′E, 55°03–12′N	1–8	Winstedt	1923
C. trinervis		Denmark	Øst-Jylland	Riebe, Fanø, near Pælebjerg	08°25′E, 55°23′N	5	Lye	20191
C. trinervis		Denmark	Øst-Jylland	Riebe, Fanø, below Pælebjerg	08°25′E, 55°23′N	6	Lye	20193
C. trinervis	590	Denmark	Øst-Jylland	Riebe, west side of Fanø	08°25′E, 55°23′N	3	Lye	29312
C. trinervis	593	Denmark	Øst-Jylland	Riebe, west side of Fanø	08°25′E, 55°23′N	2	Lye	29315
Carex × *halophila*		Finland	Oulun lääni	Haukipudas, Kello	25°21′18″E, 65°06′15″N	0.5	Lye	18578

the only taxon not studied in our AFLP analyses. Two populations of *C.* × *halophila* from coastal Finland (near the population studied anatomically) were included in an unpublished AFLP analysis. *Carex* × *halophila* is often considered a good species, but it has low fertility and is intermediate between *C. paleacea* and *C. aquatilis*, and in an unpublished AFLP study, it was found to be very close to *C. paleacea*.

Scanning electron microscopy (SEM)

Sections from the middle part of mature leaves were cut from herbarium plants and mounted on SEM stubs with epoxy, carbon coated tape. Samples were then coated with a platinum–palladium mixture in a sputter coater and pictures were taken of both adaxial and abaxial leaf surfaces at magnifications between 100× and 3000× using a Zeiss EVO 50 series SEM. Stomatal density (number of stomata per unit area for those parts of the leaves having stomata) of both leaf surfaces was measured from micrographs of 3–5 plants for each species.

Results

A detailed account of the characteristics of the leaf epidermis (Fig. 1–30) is given in Table 2 and 3. Prickle hairs are common on the margin and prominent ribs in many species, but may be present on other leaf parts too. For all species stomata are paracytically arranged in longitudinal rows parallel to the long axis of the leaf, and separated by one to several intercostal cells. The distribution of stomata on the leaf epidermis divided the investigated plants into three groups:

Epistomous leaves

This group had the lowest number of taxa, viz. *C. nigra* var. *nigra*, *C. nigra* var. *juncea* and *C. subspathacea*. *Carex nigra* (Fig. 1a, 2a) has 20–120 µm spines on the margin and on the two prominent ribs, *C. subspathacea* (Fig. 5a) does not have any spines or prickles on any of the leaf surfaces. The adaxial surface is densely set with ca 500 mm^{-2} stomata together with 7–20 µm long papillae in both species (Fig. 1b, 2b, 5b). The abaxial side does not

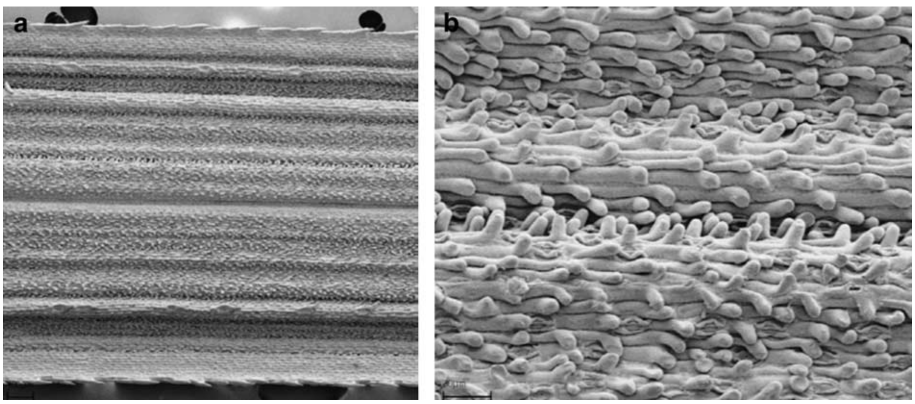

Figure 1. *C. nigra*. var. *nigra*. (a) adaxial leaf surface, from Lye 28322 (Hvaler, Asmaløy), scale = 100 µm, (b) close-up of adaxial leaf surface, from Lye 28322 (Hvaler, Asmaløy), scale = 30 µm.

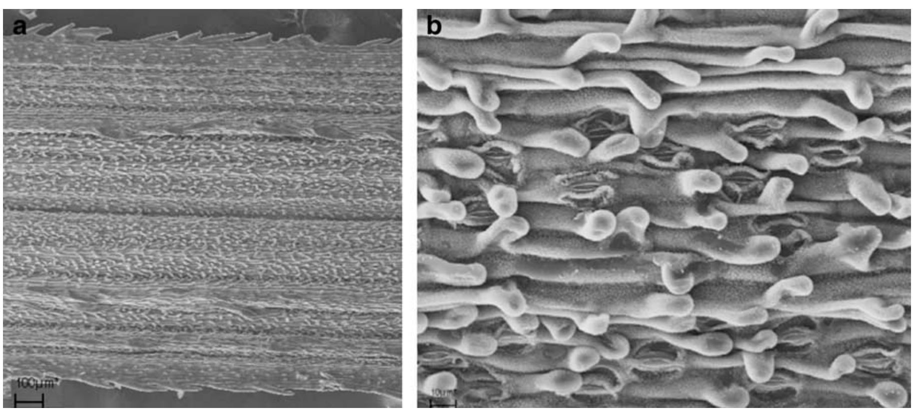

Figure 2. *C. nigra* var. *juncea*. (a) adaxial leaf surface, from Lye 28524 (Saltdal, Junkerdal), scale = 100 µm, (b) close-up of adaxial leaf surface, from Lye 28524 (Saltdal, Junkerdal), scale = 10 µm.

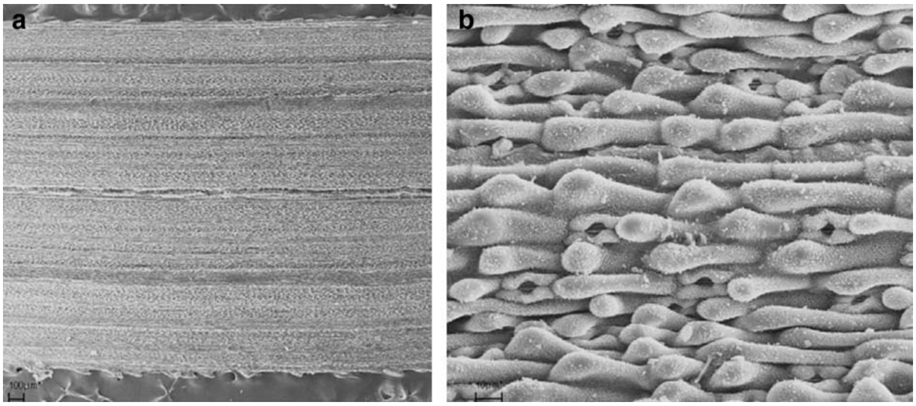

Figure 3. *C. trinervis.* (a) adaxial leaf surface, from Lye 29313 (Denmark), scale = 100 µm, (b) close-up of adaxial leaf surface, from Lye 29313 (Denmark), scale = 10 µm.

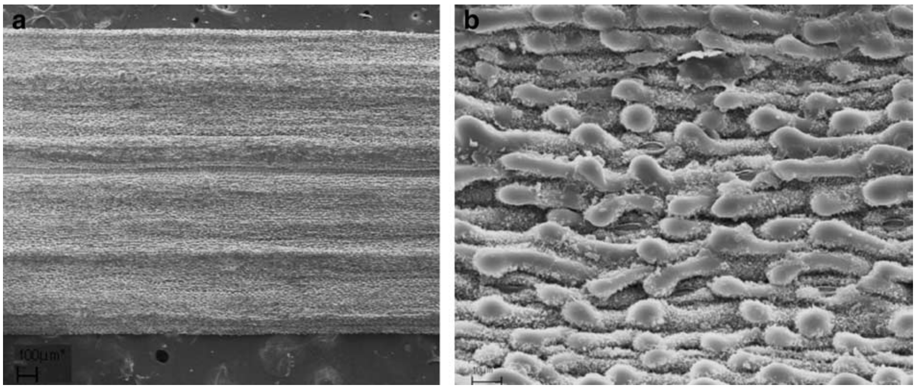

Figure 4. *C. rufina.* (a) adaxial leaf surface, from Lye 17201 (Geiranger), scale = 100 µm, (b) close-up of adaxial leaf surface, from Lye 17201 (Geiranger), scale = 10 µm.

have stomata in any of the taxa, except for some *C. nigra* var. *nigra* and *C. nigra* var. *juncea* that have a few stomata near the margins, and most examined specimens have papillae that are not very prominent.

However, it is important to note that there were forms that deviated from the epistomic condition in *C. nigra*, viz. the collection Lye 30733 from Tromsdalen that was hypostomous, while Lye 30735 from Tromsdalen and Nakamatte 28706 from Svanvik were amphistomous.

Amphistomous leaves

The adaxial side of species in this group has stomata and 5–10 µm long papillae, i.e. *C. trinervis* (Fig. 3a–b),

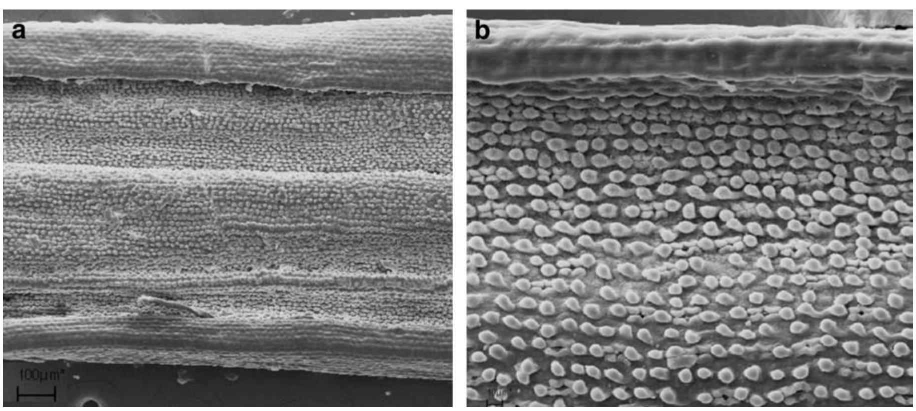

Figure 5. *C. subspathacea.* (a) adaxial leaf surface, from Lye 28429 (Skogsfjord), scale = 100 µm, (b) close-up of adaxial leaf surface, from Lye 28415 (Tromsø), scale = 10 µm.

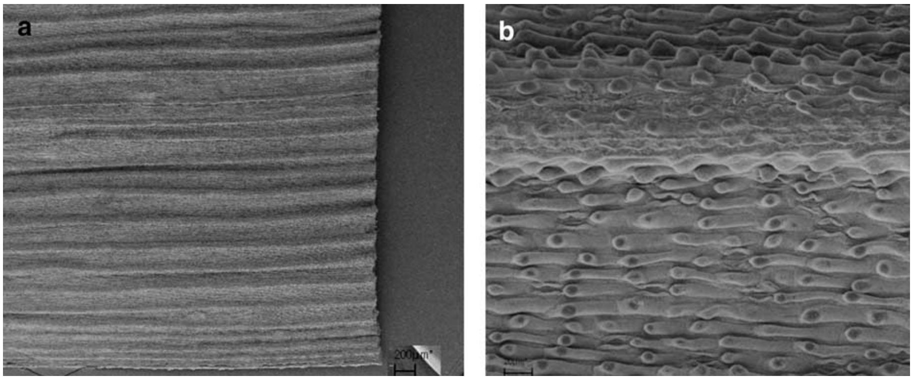

Figure 6. *C. aquatilis*. (a) adaxial leaf surface, from Lye 30732 (Enontekio, Finland), scale = 200 μm, (b) close-up of adaxial leaf surface, from Lye 30732 (Enontekio, Finland), scale = 20 μm.

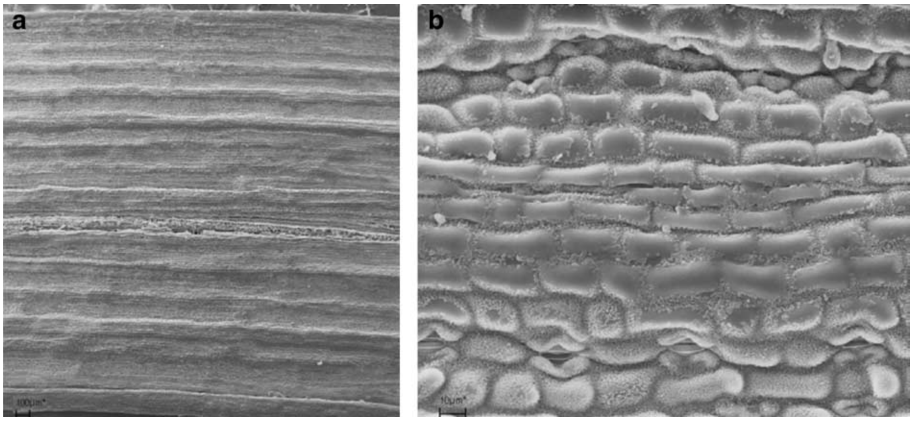

Figure 7. *C. stans*. (a) adaxial leaf surface, from Westergaard 4634 (Greenland), scale = 100 μm, (b) close-up of adaxial leaf surface, from Westergaard 4634 (Greenland), scale = 10 μm.

C. rufina (Fig. 4a–b), *C. aquatilis* ssp. *aquatilis* (Fig. 6a–b), *C. stans* (Fig. 7a–b) and *C.* × *halophila* (Fig. 8a–b). Prickles are present at the margin and on the ribs in *C. trinervis*, usually present at the leaf tip in *C. rufina*, at the margin only in *C. aquatilis* and absent in *C. stans* and *C.* × *halophila*.

The abaxial side is similar to the adaxial side and is set with stomata and 5–10 μm long papillae in *C. trinervis* (Fig. 18a–b), *C. rufina* (Fig. 19a–b), *C. aquatilis* ssp. *aquatilis* (Fig. 21a–b), *C. stans* (Fig. 22a–b) and *C.* × *halophila* (Fig. 23a–b). Stomatal density ranged between 200 and 650 mm^{-2}.

For *C. aquatilis* amphistomy was the most common condition. However, there were forms that were epistomous (Aq1024).

Hypostomous leaves

Nearly half of investigated taxa are in this group. Except for some specimens of *C. elata* that had obscure papillae, the adaxial side of the species in this group does not have prominent papillae or stomata: *C. acuta* (Fig. 9a–b),

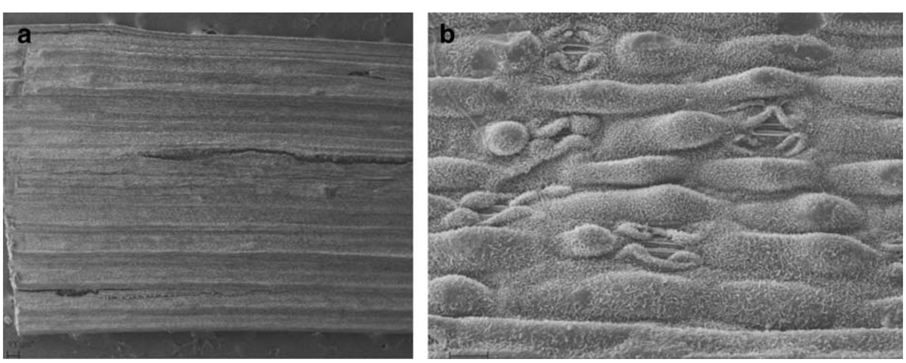

Figure 8. *C.* × *halophila*. (a) adaxial leaf surface, from Lye 18578 (Oulun lääni, Finland), scale = 100 μm, (b) close-up of adaxial leaf surface, from Lye 18578 (Oulun lääni, Finland), scale = 10 μm.

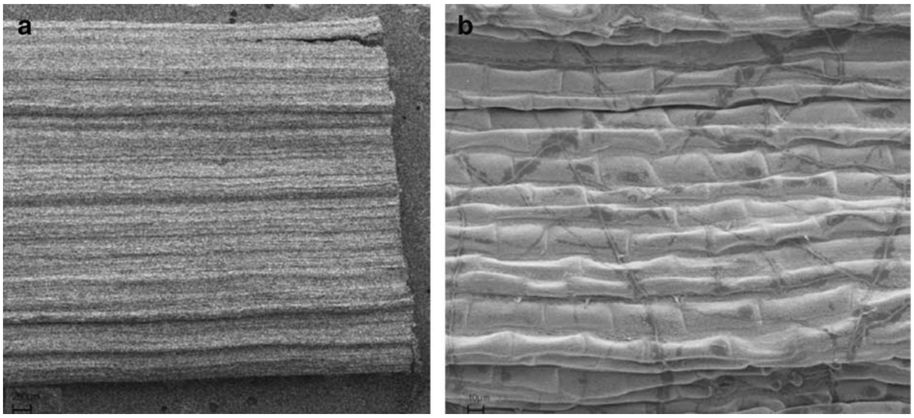

Figure 9. *C. acuta.* (a) adaxial leaf surface, from Lye 28574 (Ringebu), scale = 200 μm, (b) close-up of adaxial leaf surface, from Lye 28574 (Ringebu), scale = 10 μm.

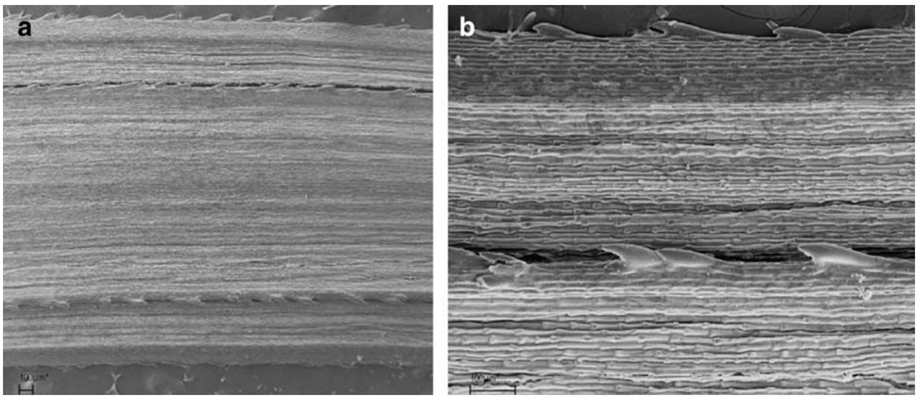

Figure 10. *C. elata.* (a) adaxial leaf surface, from Nakamatte 28354 (Semsvatn), scale = 100 μm, (b) close-up of adaxial leaf surface, from Nakamatte 28354 (Semsvatn), scale = 100 μm.

C. elata (Fig. 10a–b), *C. paleacea* (Fig. 11a–b), *C. bigelowii* ssp. *bigelowii* (Fig. 12a–b), *C. bigelowii* ssp. *rigida* (Fig. 13a–b), *C. cespitosa* (Fig. 14a–b) and *C. lyngbyei* (Fig. 15a–b). The species *C. acuta*, *C. elata*, *C. cespitosa* and *C. lyngbyei* usually have prickles on the margin and midrib, while in *C. paleacea* and *C. bigelowii* ssp. *bigelowii* prickles are usually absent.

The abaxial side was densely set with stomata and papillae, viz. *C. acuta* (Fig. 23a–b), *C. elata* (Fig. 25a–b), *C. paleacea* (Fig. 26a–b), *C. bigelowii* ssp. *bigelowii*

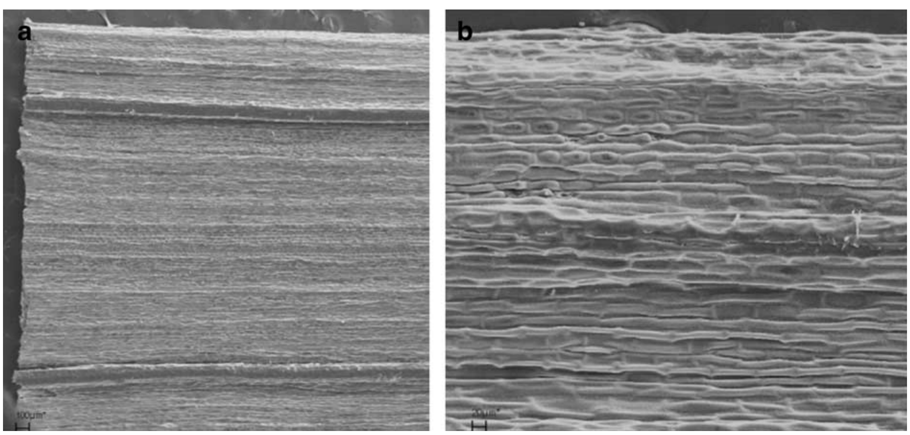

Figure 11. *C. paleacea.* (a) adaxial leaf surface, from Lye 28512 (Skaun), scale = 100 μm, (b) close-up of adaxial leaf surface, from Lye 28512 (Skaun), scale = 20 μm.

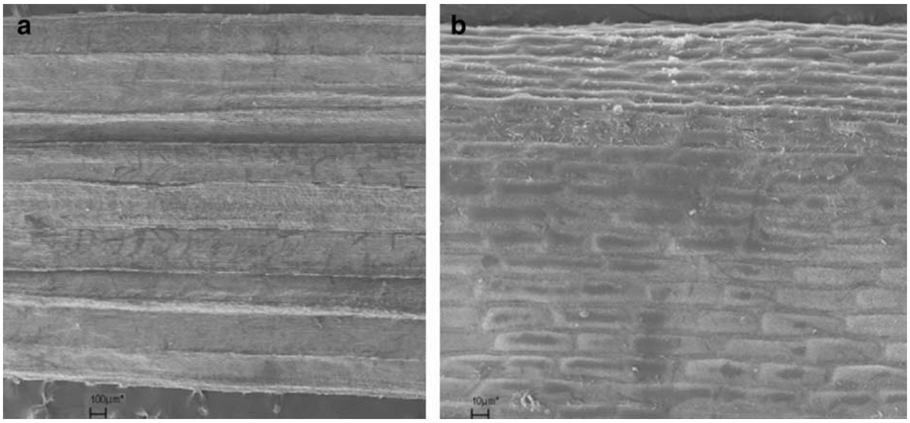

Figure 12. *C. bigelowii* ssp. *bigelowii.* (a) adaxial leaf surface, from Lye 28527 (Sulitjelma), scale = 100 μm, (b) close-up of adaxial leaf surface, from Lye 28527 (Sulitjelma), scale = 10 μm.

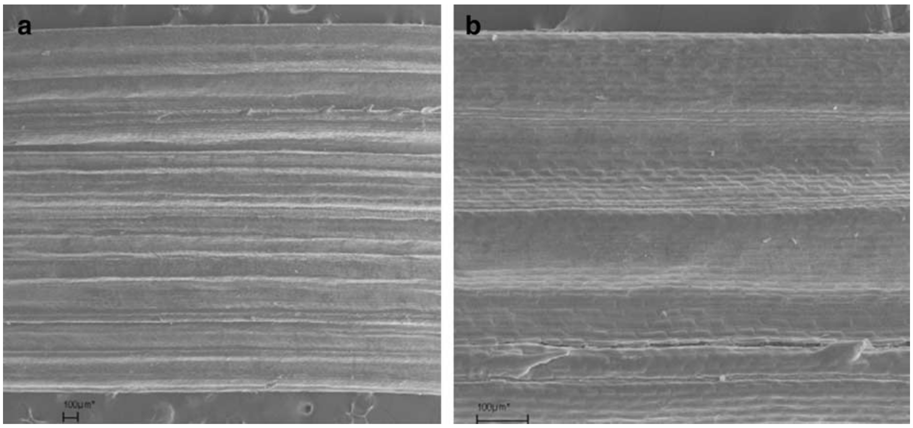

Figure 13. *C. bigelowii* ssp. *rigida.* (a) adaxial leaf surface, from Lye 28628 (Grimsdalen), scale 100 μm, (b) close-up of adaxial leaf surface, from Lye 28628 (Grimsdalen), scale = 100 μm.

(Fig. 27a–b), *C. bigelowii* ssp. *rigida* (Fig. 28a–b), *C. cespitosa* (Fig. 29a–b) and *C. lyngbyei* (Fig. 30a–b). Papillae were between 7 and 15 μm long and stomatal density was highest in *C. elata* (1000 mm^{-2}) followed by *C. acuta* (800 mm^{-2}) and ranged between 300–500 mm^{-2} in the remaining species.

Two plants *C. lyngbyei* (Lye 30670) and *C. elata* (Lye 20179) had amphistomous leaves, although all other populations of these species had hypostomous leaves.

Discussion

Our results for stomata and papillae distribution are in agreement with earlier studies on members of section

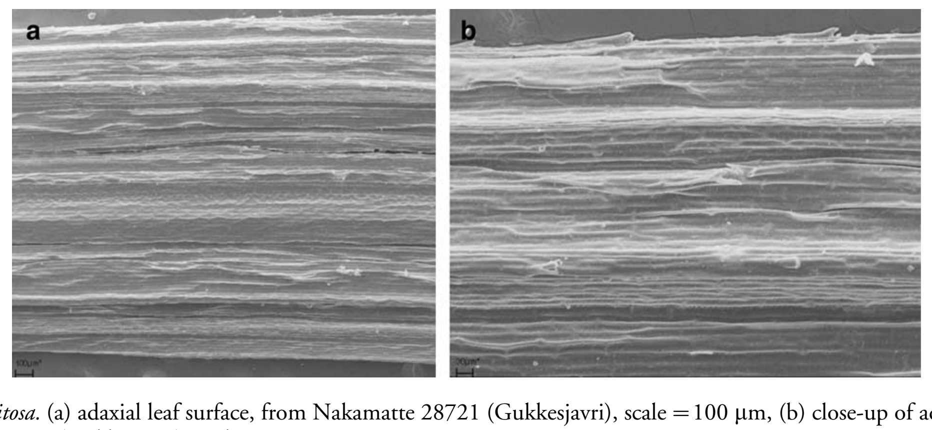

Figure 14. *C. cespitosa.* (a) adaxial leaf surface, from Nakamatte 28721 (Gukkesjavri), scale = 100 μm, (b) close-up of adaxial leaf surface, from Nakamatte 28721 (Gukkesjavri), scale = 30 μm.

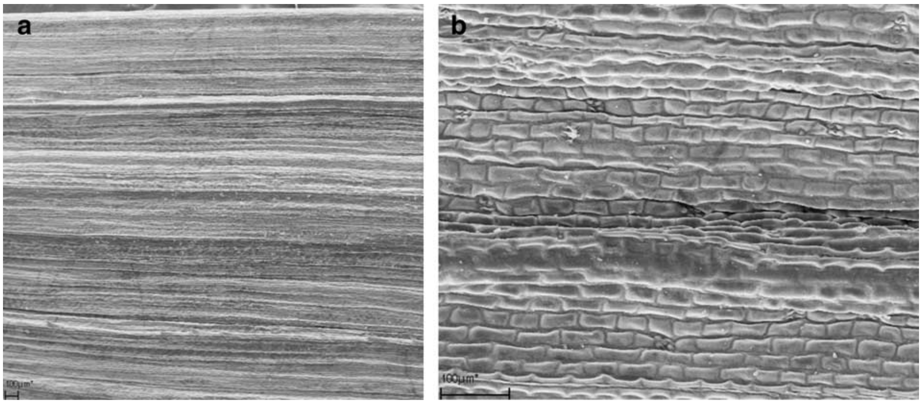

Figure 15. *C. lyngbyei.* (a) adaxial leaf surface, from Lye 30663 (south Iceland), scale = 100 μm, (b) close-up of adaxial leaf surface, from Lye 30663 (south Iceland), scale = 100 μm.

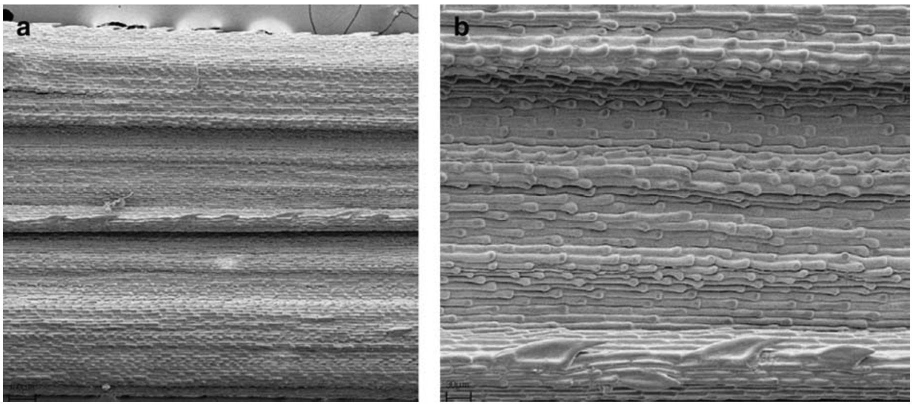

Figure 16. *C. nigra* var. *nigra.* (a) abaxial leaf surface, from Lye 28322 (Hvaler, Asmaløy), scale = 100 μm, (b) close-up of abaxial leaf surface, from Lye 28322 (Hvaler, Asmaløy), scale = 30 μm.

Phacocystis from North America and Europe (Metcalfe 1971, Standley 1987, Standley et al. 2002, Dean and Ashton 2008). However, only some of the taxa included here had been investigated previously.

Carex nigra showed most variability in stomata distribution, because forms that had all three types of stomata distribution were found, although the epistomic condition, which is reported in previous studies (Standley 1987, Dean and Ashton 2008), was the most common. The papillae distribution in *C. nigra* concurs with Metcalfe (1971) who reports low papilla on the abaxial side unlike recent studies (Standley 1987, Standley et al. 2002, Dean and Ashton 2008) that report the absence of papillae on the abaxial leaf surface. The form Lye 30733 from

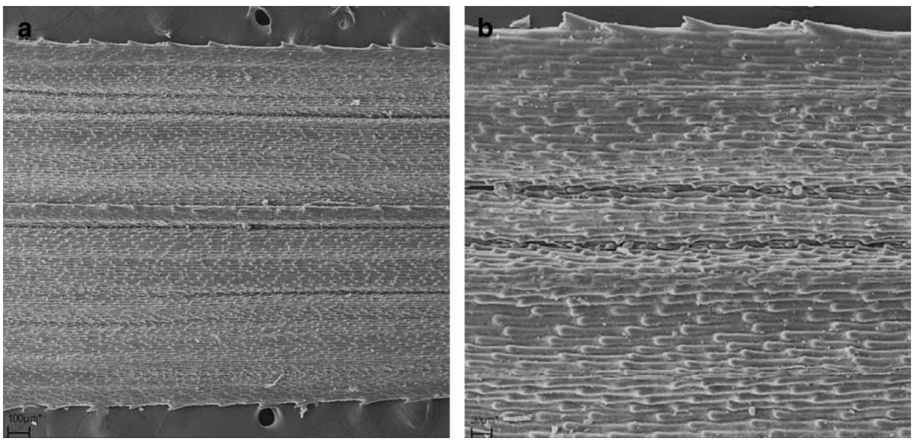

Figure 17. *C. nigra* var. *juncea.* (a) abaxial leaf surface, from Lye 28572 (Ringebu), scale = 100 μm, (b) close-up of abaxial leaf surface, from Lye 28572 (Ringebu), scale = 30 μm.

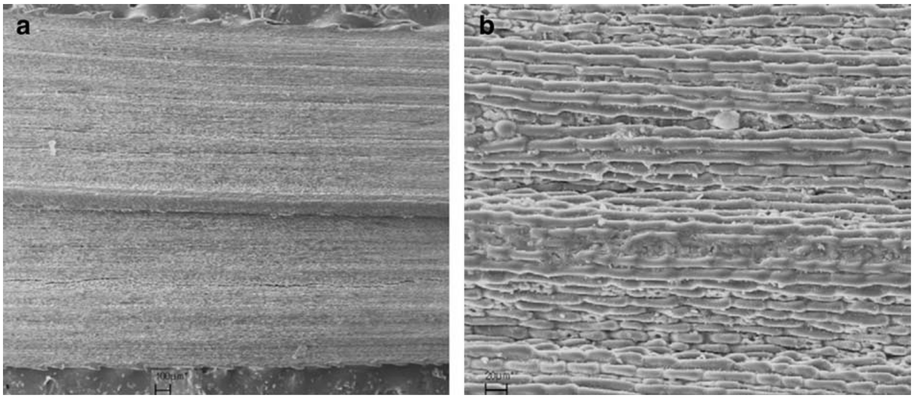

Figure 18. *C. trinervis.* (a) abaxial leaf surface, from Lye 29313 (Denmark), scale = 100 μm, (b) close-up of abaxial leaf surface, from Lye 29313 (Denmark), scale = 20 μm.

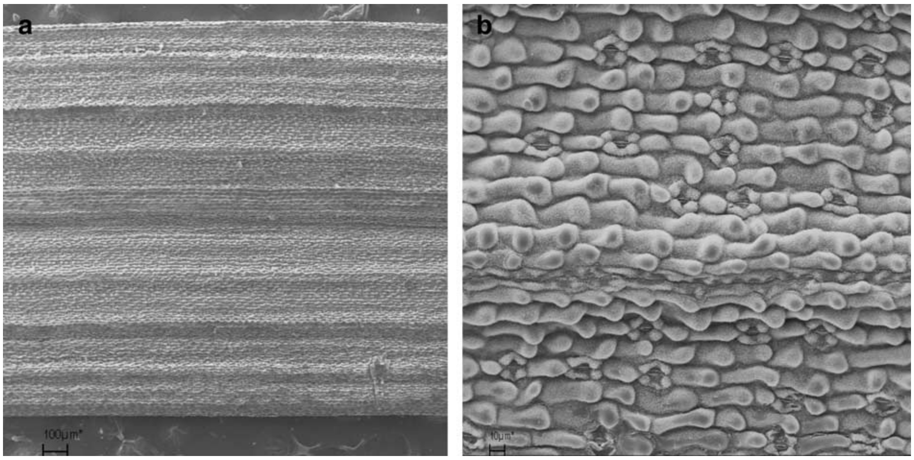

Figure 19. *C. rufina.* (a) abaxial leaf surface, from Lye 17201 (Geiranger), scale = 100 μm, (b) close-up of abaxial leaf surface, from Lye 17201 (Geiranger), scale = 10 μm.

Tromsdalen in Norway, which was hypostomous, is from an alpine race that is also genetically and morphologically slightly differentiated.

The presence of low papillae on the adaxial side in some specimens of *C. elata*, but smooth in others, is congruent with both Dean and Ashton (2008) and Crawford (1910). The former found *C. elata* adaxial side smooth, while the later described it as having papillae.

The most common condition of *C. aquatilis* found by us was the amphistomous condition, but stomatal density was generally higher on the adaxial leaf surface. These results corroborate Standley (1986), but disagree with Dean

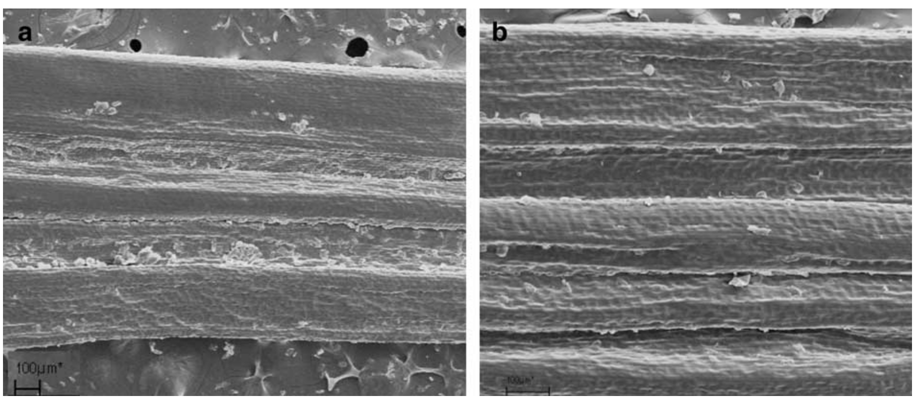

Figure 20. *C. subspathacea.* (a) abaxial leaf surface, from Lye 28429 (Skogsfjord), scale = 100 μm, (b) close-up of abaxial leaf surface, from Lye 28415 (Tromsø), scale = 100 μm.

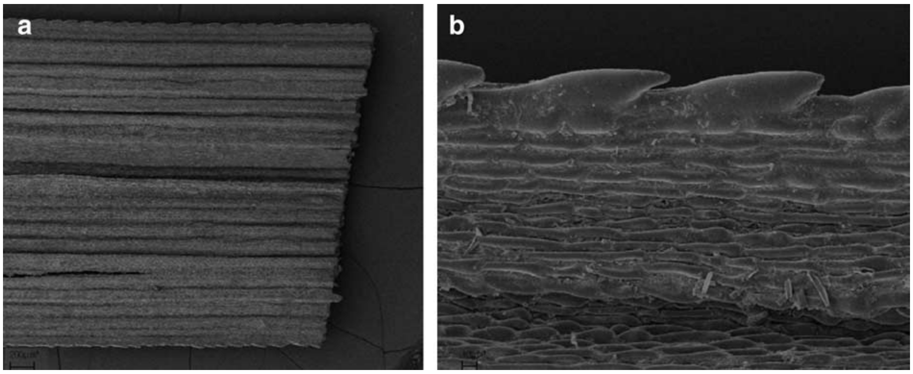

Figure 21. *C. aquatilis.* (a) abaxial leaf surface, from Nakamatte 28692 (Nordbotten), scale = 100 μm, (b) close-up of abaxial leaf surface, from Nakamatte 28692 (Nordbotten), scale = 10 μm.

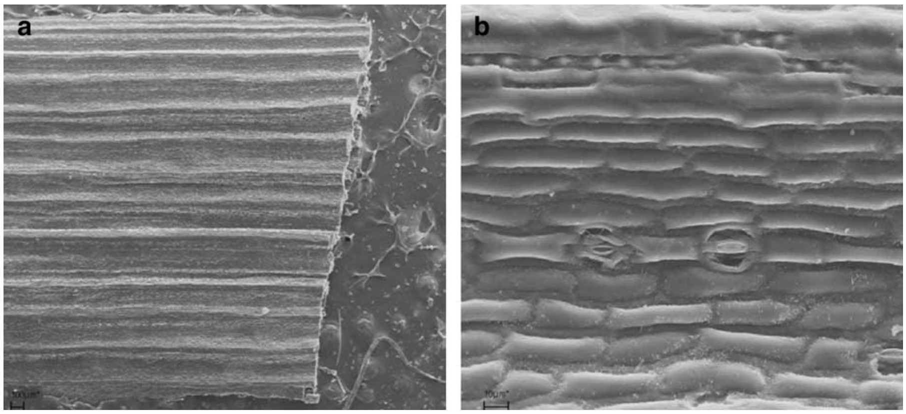

Figure 22. *C. stans.* (a) abaxial leaf surface, from Westergaard 30084 (Greenland), scale = 100 μm, (b) close-up of abaxial leaf surface, from Westergaard 30084 (Greenland), scale = 10 μm.

and Ashton (2008) who found *C. aquatilis* to be epistomous. According to Standley (1986), *C. aquatilis* var. *aquatilis* is amphistomous while *C. aquatilis* var. *dives* is epistomous. In our material, only one collection Aq1024 from Enontekio Finland was epistomous.

Since epistomous leaves are mainly found in aquatic plants with floating leaf-blades, it is somewhat surprising that 2–3 species in *Carex* sect. *Phacocystis* have such leaves (Table 2). However, the lack of stomata on the lower surface in *C. nigra* var. *juncea* may be an evolutionary adaptation to conditions during snow-melt and water-logged periods with frozen ground when it is at least partly submerged. Since such periods occasionally last for 12 months, the production of at least some photosynthetically active leaves reaching the water surface may be essential for survival. If this is the case, *C. nigra* var. *nigra* could be secondarily evolved to colonize less wet habitats, but retaining the epistomous condition of its

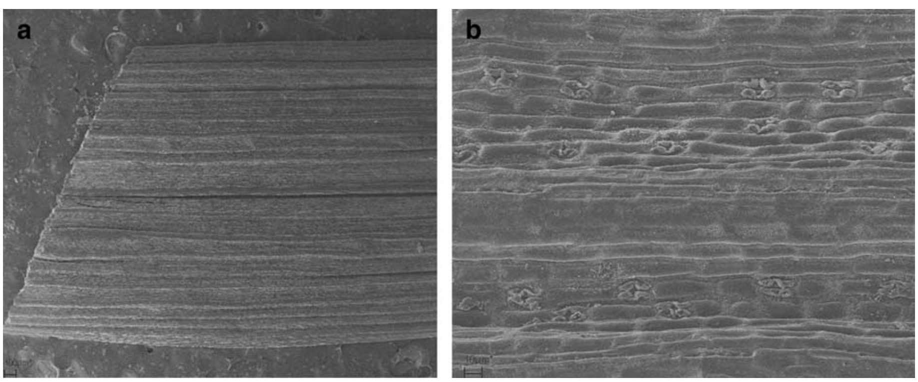

Figure 23. *C.* × *halophila.* (a) abaxial leaf surface, from Lye 18578 (Oulun lääni, Finland), scale = 100 μm, (b) close-up of abaxial leaf surface, from Lye 18578 (Oulun lääni, Finland), scale = 10 μm.

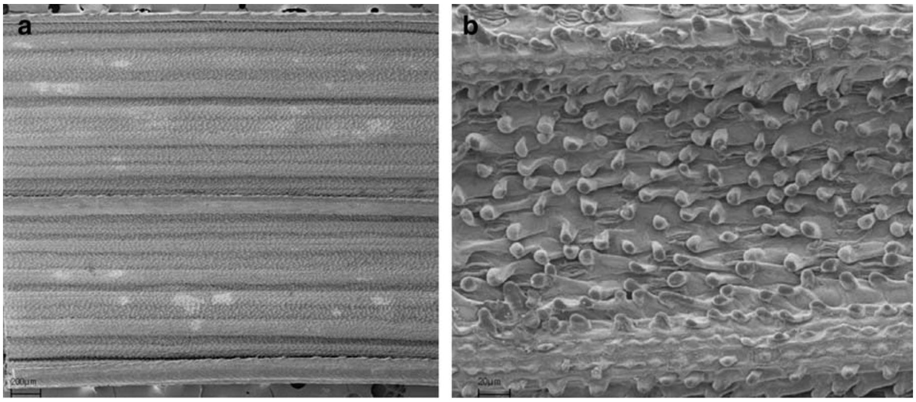

Figure 24. *C. acuta.* (a) abaxial leaf surface, from Lye 28574 (Ringebu), scale = 200 μm, (b) close-up of abaxial leaf surface, from Lye 28574 (Ringebu), scale = 20 μm.

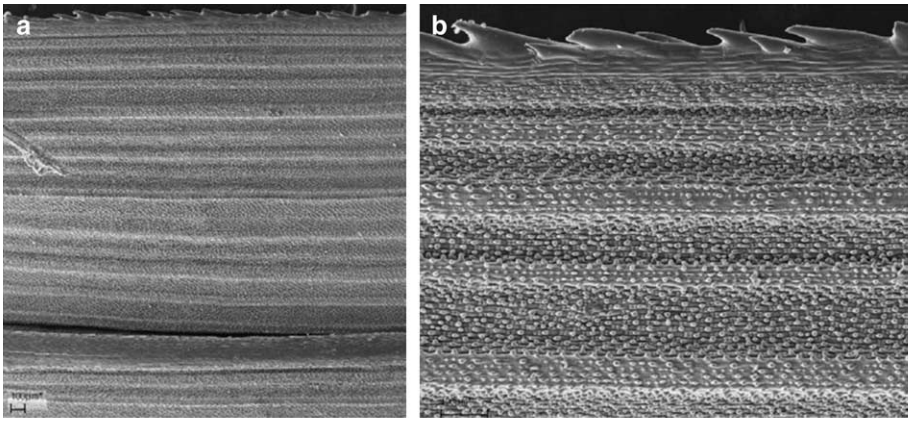

Figure 25. *C. elata.* (a) abaxial leaf surface, from Lye 27992 (Røytjern), scale = 100 μm, (b) close-up of abaxial leaf surface, from Lye 27992 (Røytjern), scale = 100 μm.

ancestors. The epistomous condition in *C. subspathacea* is ecologically easy to interpret since in its tidal marine habitats the plants are submerged twice every day. Also the occurrence of stomata on the upper side of leaves in the mostly amphistomous species *C. aquatilis* (rarely epistomous) may be an adaptation to the plants being occasionally submerged during snow-melt. On the other hand, for plants with erect or spreading leaves, it may not be important whether the stomata are on the upper or lower side. However, in sunny weather the filmy water-layer on the upper leaf-side will dry more quickly than that on the lower side, thus lengthening the photosynthetic period of an emerging submerged leaf-blade with stomata on the upper side.

Because occurrence of prominent papillae on the leaf surface is tightly linked to the presence of stomata

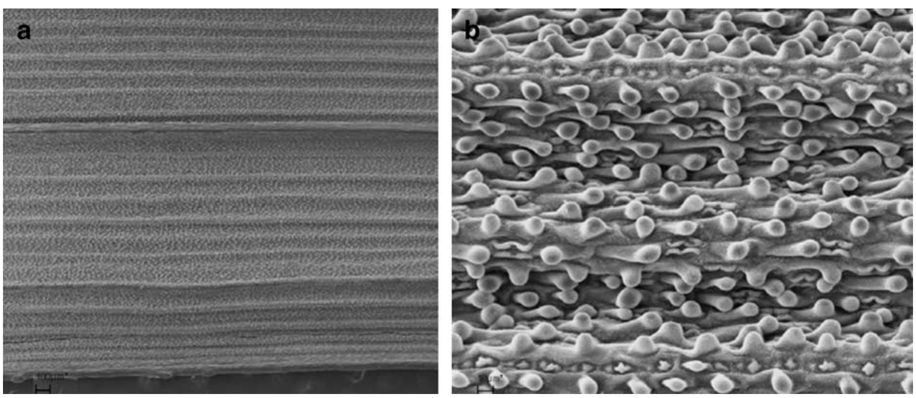

Figure 26. *C. paleacea.* (a) abaxial leaf surface, from Lye 28512 (Skaun), scale = 100 μm, (b) close-up of abaxial leaf surface, from Lye 28512 (Skaun), scale = 10 μm.

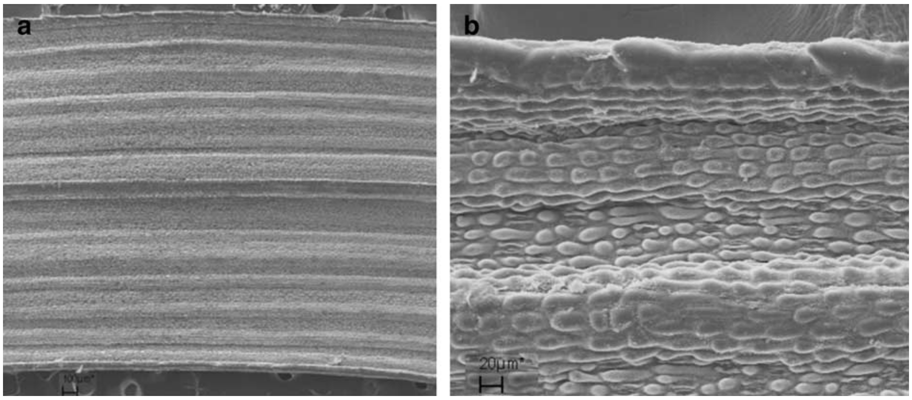

Figure 27. *C. bigelowii* ssp. *bigelowii*. (a) abaxial leaf surface, from Lye 28527 (Sulitjelma), scale = 100 µm, (b) close-up of abaxial leaf surface, from Lye 28527 (Sulitjelma), scale = 20 µm.

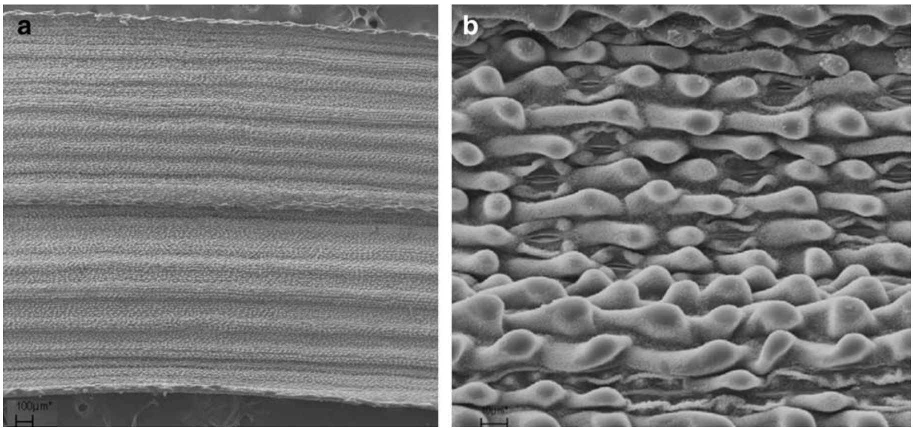

Figure 28. *C. bigelowii* ssp. *rigida*. (a) abaxial leaf surface, from Lye 28522 (Rana, Polar circle), scale = 100 µm, (b) close-up of abaxial leaf surface, from Lye 28522 (Rana, Polar circle), scale = 10 µm.

(Table 2–3), the function of the papillae is probably related to the function of the stomata or to the photosynthesis. A possible effect is the reduction of transpiration because the papillae act as hairs providing a damper environment over the stomata by reducing air-movements (Eschrich 1995). The papillose epidermis may also guide the light to the chloroplasts in the interior of the leaf (Lee 1986, Vogelmann et al. 1996).

Intercostal cells were generally smaller on the sides that had stomata and were smallest on the abaxial side of *C. elata* which had the highest stomatal density (Table 3). High stomatal density for *C. elata* and *C. acuta* was also

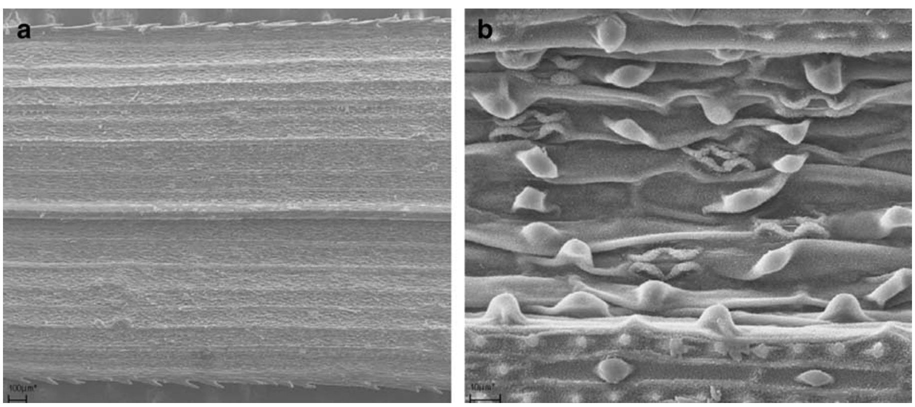

Figure 29. *C. cespitosa*. (a) abaxial leaf surface, from Nakamatte 28693 (Tervola), scale = 100 µm, (b) close-up of abaxial leaf surface, from Lye 20177 (Åmølle), scale = 10 µm.

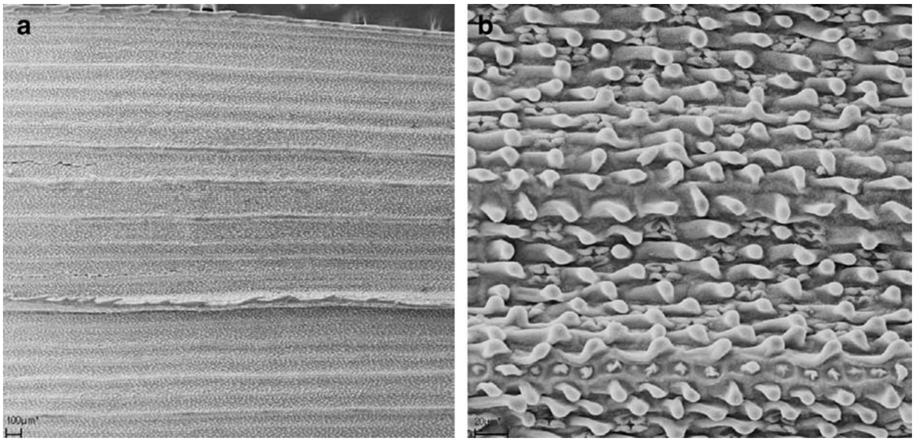

Figure 30. *C. lyngbyei*. (a) abaxial leaf surface, from Lye 30603 (southwest Iceland), scale = 100 µm, (b) close-up of abaxial leaf surface, from Lye 30603 (southwest Iceland), scale = 20 µm.

Table 2. Characteristics of the adaxial leaf epidermis of *Carex* section *Phacocystis* species from northern Europe revealed by scanning electron microscopy.

Species	Adaxial surface					
	Papillae (µm)	Stomata density range (mm^{-2})	Mean stomata density (mm^{-2})	Intercostal cells (L × W) µm	Prickles (µm); position	Figure
C. nigra var. *nigra*	9–19	500–600	512	30–90 × 5–9	25–120; on ribs and margin	1a–b
C. nigra var. *juncea*	7–14	350–775	500	70–90 × 6–8	20–50; on ribs and margin	2a–b
C. trinervis	9–12	200–600	500	25–65 × 6–9	18–30; on ribs and margin	3a–b
C. rufina	7–11	200–366	265	20–35 × 5–12	20–60; at leaf tip	4a–b
C. subspathacea	7–9	130–725	520	15–17 × 2–5	absent	5a–b
C. aquatilis	8–9	350–550	450	53–56 × 8–10	40; on margin	6a–b
C. stans	5–7	20–633	525	18–32 × 7–9	absent	7a–b
Carex × *halophila*	6–7	350–500	425	25–50 × 6–8	absent	8a–b
C. acuta	absent	0	0	28–38 × 7–14	28–30; on ribs and margin	9a–b
C. elata	absent/ obscure	0	0	60–90 × 8–10	20–62; on ribs and margin	10a–b
C. paleacea	absent	0	0	40–120 × 6–10	absent	11a–b
C. bigelowii ssp. *bigelowii*	absent	0	0	28–64 × 12–14	absent	12a–b
C. bigelowii ssp. *rigida*	absent	0	0	28–43 × 12–14	absent	13a–b
C. cespitosa	absent	0	0	65–75 × 7–11	20–80; on ribs and margin	14a–b
C. lyngbyei	absent/ obscure	0–20	5	35–65 × 10–20	15–50; on ribs and margin	15a–b

recorded by Dean and Ashton (2008). Intercostal cell lengths and widths have been found to be of taxonomic significance (Dean and Ashton 2008) and proved useful for final identification in some of the investigated species, but were overlapping in several species.

If we compare micro-morphological characters of leaves with general morphological structures, we find that micro-morphological characters sometimes better correspond to molecular data, e.g. *C. rufina* can morphologically be considered an alpine dwarf-form of *C. nigra*, but their micro-morphology is very different as *C. rufina* has prominent papillae and stomata, but no prickles on abaxial leaf epidermis, while *C. nigra* has prickles, but neither papillae nor stomata on the lower leaf-surface (Table 3). Similarly, *C. cespitosa* and *C. nigra* var. *juncea* (both forming dense tussocks) differ in that *C. cespitosa* has prominent papillae and stomata on lower leaf surfaces, while these are lacking in *C. nigra*. Among other species there is good correspondence between morphological and micro-morphological characters, e.g. *C. trinervis* and *C. acuta*, which in the molecular analysis (Nakamatte and Lye 2007) form a neighbour pair, and are both morphologically and micro-morphologically (Table 2) well separated. Unfortunately, in Scandinavia the most common and widespread species, i.e. *C. nigra* and *C. aquatilis*, are also both morphologically and micro-morphologically the most variable species, but the unusual or divergent anatomical forms are rare.

With reference to groupings from cytogenetics (Faulkner 1973), DNA (Nakamatte and Lye 2007) and generally known taxonomic relationships of species in section *Phacocystis*, the groups from leaf micro-morphological characters of the investigated species seem to be important in distinguishing individual species but not in subsectional classification.

Table 3. Characteristics of the abaxial leaf epidermis for *Carex* section *Phacocystis* species from North Europe revealed by scanning electron microscopy.

Species	Abaxial surface					
	Papillae (μm)	Stomata density range (mm^{-2})	Mean stomata density (mm^{-2})	Intercostal cells (L × W) μm	Prickles (μm); position	Figure
C. nigra var. *nigra*	absent/ obscure	0	0	45–100 × 6–10	25–120; on margin and midrib	16a–b
C. nigra var. *juncea*	absent/ obscure	0	0	40–90 × 7–9	20–50; on margin and midrib	17a–b
C. trinervis	7–14	250–333	299	20–50 × 7–10	18–30; on margin and midrib	18a–b
C. rufina	4–9	190–386	300	35–45 × 4–7	absent	19a–b
C. subspathacea	absent	0	0	20–50 × 9–25	absent	20a–b
C. aquatilis	5–10	233–550	390	55 × 7	40; on margin	21a–b
C. stans	2–5	410–850	630	20–45 × 6–13	Absent	22a–b
Carex × *halophila*	2–5	280–500	350	15–50 × 5–9	Absent	23a–b
C. acuta	9–12	700–900	800	35–55 × 12–18	28–30; on margin and midrib	24a–b
C. elata	7–14	600–1500	1000	24–34 × 4–7	20–62; on margin and midrib	25a–b
C. paleacea	10–14	400–600	516	25–60 × 6–10	50–100; on margin	26a–b
C. bigelowii ssp. *bigelowii*	7–12	450–600	516	22–45 × 6–10	16–23; on margin	27a–b
C. bigelowii ssp. *rigida*	8–14	250–675	416	29–44 × 5–7	57; on margin and midrib	28a–b
C. cespitosa	7–12	200–400	297	49–68 × 16–19	20–80; on margin and midrib	29a–b
C. lyngbyei	8–15	450–990	700	25–35 × 7–10	15–50; on margin and midrib	30a–b

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