The taxonomic and phylogenetic utility of vegetative anatomy and fruit epidermal silica bodies in *Carex* section *Phyllostachys* (Cyperaceae)

Julian R. Starr and Bruce A. Ford

Abstract: In *Carex*, vegetative anatomy and fruit epidermal silica bodies have been used to delimit species and sections, although frequent conflicts with traditional classifications have led many authors to question whether they can be used to infer evolutionary relationships. This conclusion, however, has largely been drawn from poorly circumscribed groups that have not been phylogenetically analyzed. This study was undertaken to assess the taxonomic and phylogenetic utility of these characters within *Carex* section *Phyllostachys*, a small (eight species), monophyletic group whose taxonomy and phylogeny has been extensively studied. Leaf and culm anatomy clearly separate the close species pair of *Carex backii* Boott and *Carex saximontana* Mackenzie, and they provide unique characters that distinguish *Carex latebracteata* Waterfall and *Carex juniperorum* Catling, Reznicek, & Crins. Anatomical and silica body characters strongly support the recognition of three species within the *Carex willdenowii* Willdenow complex (*Carex willdenowii* s.s., *Carex basiantha* Steudel, *Carex superata* Naczi, Reznicek, & B.A. Ford). Although unique characters were lacking in *Carex jamesii* Schw., infraspecific variation in its silica bodies was consistent with the high levels of genetic and morphological variation previously detected. Silica body characters support groups that are congruent with previous phylogenetic hypotheses derived from both morphological and molecular data. In contrast, vegetative anatomy, in this and previous studies, supports contradictory groups suggesting that its use in future phylogenetic studies below the sectional level in *Carex* may be limited.

Key words: *Carex*, anatomy, silica bodies, cladistics, species circumscription.

Résumé : Chez les *Carex*, l'anatomie végétative et les corps siliceux de l'épiderme du fruit ont été utilisés pour délimiter les espèces et les sections, bien que de nombreux conflits avec les classifications traditionnelles aient conduit plusieurs auteurs à remettre en question leur utilité pour déduire les filiations évolutives. Cependant, cette conclusion a été tirée surtout à partir de groupes mal définis dont la phénologie n'a pas été analysée. Les auteurs ont entrepris cette étude pour évaluer l'utilité taxonomique et phylogénétique de ces caractères pour les *Carex* de la section *Phyllostachys*, un petit groupe (8 spp.) monophylétique dont la taxonomie et la phylogénie ont été largement étudiées. L'anatomie de la feuille et du chaume séparent nettement les paires d'espèces voisines *Carex backii* Boott et *Carex saximontana* Mackenzie, et fournissent des caractères uniques qui distinguent les *Carex latebracteata* Waterfall et *Carex juniperorum* Catling, Reznicek, & Crins. Les caractères anatomiques et les corps siliceux supportent fortement la reconnaissance de trois espèces au sein du complexe *Carex willdenowii* Willdenow (*Carex willdenowii* s.s., *Carex basiantha* Steudel, *Carex superata* Naczi, Reznicek, & B.A. Ford). Bien qu' il n'y aie pas de caractères distinctifs pour le *Carex jamesii* Schw., la variation infraspécifique de ses corps siliceux correspond aux degrés élevés de variation morphologique et génétique déjà perçus. Les caractères des corps siliceux supportent des groupes qui concordent avec des hypothèses phylogénétiques antécédentes dérivées à la fois de données morphologiques et moléculaires. Au contraire, les caractères de l'anatomie végétative, dans cette études et dans des études antécédentes, supportent des groupes contradictoires, ce qui suggère que leur usage devrait être limité dans les études phylogénétiques futures, en dessous du niveau de la section, chez les *Carex*.

Mots clés : *Carex*, anatomie, corps siliceux, cladistique, délimitation des espèces.

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Introduction

The Cyperaceae has long been recognized as one of the most taxonomically challenging angiosperm families because of its great diversity (ca. 5000 species; Bruhl 1995), highly reduced flowers, and complex character evolution (Reznicek 1990; Starr et al. 1999). Two seminal studies in the 1970s involving the first extensive survey of leaf, culm, and epidermal anatomy (Metcalfe 1971) and the first examination of fruit epidermal silica bodies (Schuyler 1971) held the promise that the systematics of the family could be reevaluated with a new set of conserved characters. In *Carex* L., the largest genus (ca. 2000 species), these characters were successfully used to circumscribe species (e.g., Toivonen and Timonen 1976; Wujek and Menapace 1986; Ford and Ball 1992) and even sections (e.g., Walter 1975; Menapace and Wujek 1987; Toivonen and Timonen 1976; Menapace et al. 1986; Crins and Ball 1988). However, it soon became apparent that many groups circumscribed on the basis of anatomical and (or) silica body characters conflicted significantly with taxa delimited on the basis of morphology and other features (e.g., Shepherd 1976; Standley 1987, 1990; Waterway 1990; Ford et al. 1991; Ford and Ball 1992). This led some authors to conclude that homoplasy in anatomical and silica body characters was high (Rettig 1986; Standley 1990; Waterway 1990) and, consequently, that they were unreliable indicators of evolutionary relationship (Rettig 1986; Waterway 1990; Ford and Ball 1992). It is important to note, however, that these conclusions were drawn from groups that had not been phylogenetically analyzed. When anatomical and silica body characters were eventually used with morphology in the cladistic analysis of *Carex* section *Griseae* (18 species; Naczi 1992), they provided characters that were essential to the definition of several small clades. Consequently, the question is raised as to whether anatomical and silica body characters are inherently unreliable or whether previous negative conclusions regarding their phylogenetic utility in *Carex* can be explained by factors such as personal bias, poor circumscription, or limited sampling.

Small groups can make significant contributions to the systematics of large and complex taxa like *Carex* because factors such as poor sampling and circumscription can be minimized, whilst the accuracy of results can be reasonably assessed through the congruence of multiple data sets. It is for these reasons that *Carex* section *Phyllostachys* (J. Carey) L.H. Bailey, a small, monophyletic group of eight species, has been the focus of a series of evolutionary studies that have explored the influence of historical and biological factors on its genetic diversity (Ford et al. 1998*a*, 1998*b*) and that have widely examined the cladistic relationships of its species using morphology, nuclear ribosomal DNA internal transcribed spacer (ITS) sequences, and isozymes (Crins 1990; Starr 1997; Ford et al. 1998*a*; Starr et al. 1999). While some relationships in the section remain unresolved (e.g., Naczi and Ford 1998), enough is known about the phylogeny and taxonomy of the *Phyllostachys* that it can serve as a reasonable model for assessing homoplasy levels in anatomical and silica body characters within *Carex*.

Carex section *Phyllostachys* is a typical group in *Carex* in that the morphological characters used to distinguish its species are largely quantitative and continuous. For example, despite distinct genetic differentiation among the three species of the *Carex willdenowii* Willdenow complex (i.e., *Carex basiantha* Steudel, *Carex superata* Naczi, Reznicek, & B.A. Ford, *Carex willdenowii* s.s.; Ford et al. 1998*c*), its members can only be distinguished morphologically by a set of height and length differences in mature reproductive structures (Naczi et al. 1998). Similarly, Ford et al. (1998*b*) and Starr (1997) have shown that *Carex backii* Boott and *Carex saximontana* Mackenzie are genetically distinct, despite being separable only by subtle distinctions in the length of the anthers and perigynium beak (Catling et al. 1993). These seemingly minor differences have convinced several authors that *C. saximontana* should be treated as a variety of *C. backii* (e.g., Hudson 1977; Scoggan 1978; Boivin 1992) or that the two taxa should be merged (e.g., Moss 1983; Gleason and Cronquist 1991; Hurd et al. 1998; Wilson et al. 1999). In the above two cases, the integration of anatomical and silica body characters with the preexisting morphological and genetic data will be instructive both as to the utility of these characters for circumscribing critical groups and as evidence for or against the recognition of these taxa. The remaining species in the section (*Carex juniperorum* Catling, Reznicek, & Crins; *Carex latebracteata* Waterfall; *Carex jamesii* Schw.) are easily distinguished by several characters, though recent evidence suggests that a new taxon, closely aligned to *C. juniperorum* and *C. jamesii*, is worthy of recognition (Naczi and Ford 1998).

This paper presents a comparative study of leaf, culm, and epidermal anatomy and the micromorphology of achene epidermal silica bodies in all eight species presently recognized in *Carex* section *Phyllostachys*. The anatomy and micromorphology of a possible ninth taxon (see above) is currently being studied and will not form a part of this analysis (Naczi and Ford 1998). The purpose of this study was, first, to evaluate the taxonomic and phylogenetic potential of anatomical and silica body characters within section *Phyllostachys* and *Carex* in general, and secondly, to determine whether anatomy and silica bodies could help resolve the remaining conflicts between data sets concerning the phylogeny of section *Phyllostachys*.

Materials and methods

Anatomical studies

Anatomical studies were based upon leaf and culm samples taken from herbarium and live specimens representative of all species in *Carex* section *Phyllostachys*. For live specimens, a fully developed leaf was removed, along with culms, and placed in formalin – aceto-alcohol (FAA). Dry material was boiled in water for 5 min then placed in FAA (Radford et al. 1974). Segments 4–5 cm long were cut from the median portion of preserved leaves for both epidermal and cross-sectional studies. Culm segments 2–4 cm long were removed immediately below the point where the culm begins to dilate. This procedure was necessary because of the particularly short culms of *C. juniperorum* and *C. superata*.

Leaves and culms were hand sectioned with a razor blade. Sections were dehydrated in an ethanol series and stained while heated for 3.5 min with 2% toluidine blue O in 100% ethanol. Sections were made permanent by passing them through a 100% ethanol – Histoclear® dehydration series and by mounting them in Permount®. To increase sample size, and to determine the consis-

Table 1. Character descriptions for all variable leaf, culm, epidermal, and silica body characters scored in Table 2.

Characters	
Leaf Anatomy	1. Leaves, lightly revolute or curved (C) vs. V-shaped (V).
	2. Thickest point of lamina, = the thickness of the keel (E) vs. > keel (T).
	3. Keel, shape acute (A) vs. rounded or flat (R).
	4. Bulliform cells, = the largest epidermal cells (E) vs. > largest epidermal cells (L)
	5. Leaf margins completely (C) vs. incompletely (I) sclerified vs. both states equally (E) probable.
	6. Minor vascular bundles, often overtop (O) of air cavities vs. between (B) air cavities.
	7. Adaxial girders, often interrupted (I) by parenchymatous cells vs. completely sclerifed (S)
Culm Anatomy	8. Minor vascular bundles completely (C) within chlorenchyma vs. resting (R) against central ground tissue.
	9. Culm, highly (H) sclerified vs. typical (T).
	10. Number of angles or wings three (T) vs. three to five (F)
	11. Angles or wings, strongly (S) vs. weakly (W) sclerified.
	12. Epidermal papillae, present (P) vs. absent (A).
	13. Epidermal papillae, confined (C) to apices of angles vs. ubiquitous or sparsely distributed (U). (—) Not applicable.
	14. Epistomatal cavities, present (P) vs. absent (A).
Leaf Epidermal Surfaces	15. Number of silica bodies in cells overlying sclerenchyma girders, up to four (F) vs. as many as six (S).
	16. Silica bodies with satellites, present (P) vs. absent (A).
	17. Rows of marginal silica body cells, three (T) vs. five (F).
	18. Stomata, elliptical (E) vs. orbicular to suborbicular (O).
	19. Epistomatal cavities, present (P) vs. absent (A).
	20. Marginal prickle hairs, present (P) vs. absent (A).
	21. Marginal papillae, present (P) vs. absent (A).
	22. Papillae, present or rarely present (P) vs. absent (A) on adaxial surface.
	23. Papillae, present (P) vs. absent (A) on abaxial surface.
	24. Prickle hairs, present (P) vs. absent (A) on adaxial surface.
Silica Bodies (Micromorphology)	25. Silica platform, concave (C) vs. convex (V).
	26. Silica platform, margins thickened creating trough (T) vs. margins not thickened (N).
	27. Silica platform, distinctly raised (D) vs. raised (R). (—) Not applicable.
	28. Silica platform, ornamented (O) vs. not ornamented (N).
	29. Satellite bodies, present (P) vs. absent (A).
	30. Periclinal wall, persistent (P) vs. not persistent (N).

Note: Character states are those most commonly observed for each species. Characters are numbered in the order that they appear in the text. Consult text for the full range of variation.

tency of character states, cross sections of live material were also made and mounted in water.

Leaf epidermal surfaces were prepared by placing FAA-preserved material into a glass Petri dish containing household bleach and scraping the undesired tissue away with a razor blade. The epidermal surfaces were then passed through three 15-min water baths and stained for 3 min with 2% safranin. The epidermal surfaces were then dehydrated, cleared, and mounted as above. Epidermal photographs were taken with a microscope-mounted camera, whilst drawings of leaf cross sections were made by camera lucida. The terminology used to describe the anatomy of the leaf, culm, and epidermis follows Metcalfe (1971). Specimens used in anatomical studies are listed in Appendices 1–3.

Micromorphological studies

The lowermost, mature perigynium was removed from each of two terminal spikes from three to six specimens representative of the geographic range of each species (Appendix 4). The perigynium surrounding the achene was dissected away and the achenes were acetolyzed in a 1:9 sulfuric acid – acetic anhydride solution (Tallent and Wujek 1983). Achenes were vigorously shaken for 5 min, then left for 24–48 h in solution. At the end of this period, achenes were shaken for 5 min, removed, and then washed in distilled water by shaking for a further 5 min. Those achenes whose cell walls were still persistent after undergoing the above procedure were sonicated in distilled water at maximum probe intensity for 1.5 min with a Biosonic® sonicator (Bronwill Scientific, Rochester, N.Y.). Achenes were then dried overnight at 50°C, mounted onto aluminum stubs with conductive carbon paint (SPI® Supplies), and coated with 100–200 nm of a gold–palladium alloy in an Edwards Sputter Coater S150B. Micrographs were taken along the median portion of achenes using a Stereoscan 120 scanning electron microscope (Cambridge Instruments; 20 kV accelerating voltage) that was connected to a Kontron Elektronik IBAS image analyzer. Silica bodies were described according to the terminology of Schuyler (1971).

Results

Summary descriptions and scoring for all variable characters discovered in this study are provided in Tables 1 and 2.

Anatomy

Leaves

Leaf anatomy in *Carex* section *Phyllostachys* was relatively uniform and corresponded to a common pattern in the genus. Leaves were dorsiventrally arranged, keeled on the abaxial surface, and either V shaped or lightly revolute in cross section. All leaves possessed a single, abaxial row of vascular bundles with each bundle separated by well-developed air cavities (square or rectangular in outline) and connected to the epidermis by sclerenchymatous girders. The median vascular bundle, which was typically the largest, rested against a single, adaxial layer of bulliform cells, and like other bundles, it was surrounded by an inner sclerenchymatous and an outer parenchymatous sheath. Epidermal cells were consistently larger on the adaxial versus the abaxial surface, and cells were frequently adorned by papillae and (or) prickle hairs (see below).

Based on foliar anatomy, two broad groups were recognized in section *Phyllostachys*. The first group, composed of *C. latebracteata* and *C. saximontana*, was distinguished by a lightly revolute or curved lamina, whose thickest point was

Table 2. Character state matrix for all variable leaf, culm, epidermal, and silica body characters observed in *Carex* section *Phyllostachys*.

	Leaf anatomy							Culm anatomy							Leaf epidermal surfaces										Silica bodies (micromorphology)					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
C. backii	V	T	R	L	I	O	S	R	T	T	S	P	C	A	F	A	T	E	A	P	P	A	A	A	C	N	—	N	A	N
C. basiantha	V	T	R	L	I	O	I	R	T	T	W	A	—	A	F	A	T	E	A	P	A	A	A	P	V	N	D	O	A	N
C. jamesii	V	T	R	L	I	B	I	R	T	T	S	A	—	A	F	A	T	O	A	P	A	A	A	A	V	T	R	N	A	N
C. juniperorum	V	T	R	L	E	O	I	R	T	F	W	P	U	A	F	A	T	E	A	P	P	P	P	P	V	T	R	N	A	N
C. latebracteata	C	E	A	E	C	B	S	C	T	T	S	A	—	A	F	A	F	O	A	A	P	P	A	A	V	N	R	N	A	P
C. saximontana	C	E	A	E	C	B	S	R	T	T	S	P	U	P	F	A	T	E	P	P	P	P	P	A	C	N	—	N	A	N
C. superata	V	T	R	L	I	O	I	R	H	T	S	A	—	A	F	A	T	E	A	P	A	P	A	A	V	N	D	O	A	N
C. willdenowii	V	T	R	L	I	O	I	R	T	T	S	A	—	A	S	P	T	E	A	P	P	P	P	P	V	N	D	N	P	N

Note: Character states are those most commonly observed for each species. Characters are numbered in the order that they appear in the text. See text for the full range of variation.

equal to or less than the thickness of the keel (Figs. 1*a* and 1*b*). The keel was prominent and acute with a large, highly sclerified, horizontal to lightly descending abaxial girder that connected the median vascular bundle to the epidermis. In addition, the bulliform cells were no larger than the largest cells of the epidermis. Leaf margins were completely sclerified and were either scabrous, crenulate or smooth. While this pattern was fairly consistent in both taxa we did note some variability in *C. saximontana* with some specimens having leaf margins that were both papillose and incompletely sclerified (e.g., *Naczi 3372 & Thieret*, WIN).

The second group was distinguished by V-shaped leaves where the thickest point of the lamina was thicker than the thickness at the keel (Figs. 1*c*, 1*d*, and 2*a*–2*d*). The keel was rounded or flat, and the leaves were often lightly bowed or occasionally curled on one half of the lamina. In addition, the bulliform cells were often larger than the largest cells of the epidermis. A small sclerenchyma strand on the adaxial surface of the margin was also characteristic of these species, although *C. juniperorum* often possessed completely sclerified margins similar to *C. latebracteata* and *C. saximontana*. Two further characters, the presence of minor vascular bundles overtop of air cavities and the interruption of adaxial girders by parenchymatous cells, were frequent in this group but rare in *C. latebracteata* and *C. saximontana*. Both of these characters appeared to be related to the thickness of the leaf.

Culms

Culms of all species contained 4–10 major and 1–8 minor vascular bundles (Fig. 3). These were arranged alternately by size and in a circular or triangular fashion within a thin, chlorenchymatous zone adjacent to the epidermis. With the exception of *C. latebracteata*, in which minor bundles were completely contained within chlorenchyma (Fig. 3*a*), the xylem pole of both major and minor bundles rested against a spongy translucent ground tissue at the centre. Alternating between vascular bundles were air chambers of various sizes and shapes. In *C. superata*, these chambers were confined to the chlorenchyma of the culm angles because of the highly sclerified nature of its culm (Fig. 3*b*). As in leaves (see below), epidermal cells overlying the sclerenchyma of girders and wings frequently possessed conical silica bodies.

All culms were triangular in shape except in certain individuals of *C. juniperorum*. In this species the culm was commonly asymmetrical and possessed from three to five angles or wings (Figs. 3*c* and 3*d*). Along with *C. basiantha*, *C. juniperorum* was also unusual in that the sclerification of the wings was typically weak or absent (cf. Figs. 3*c*, 3*d*, and 3*e* with the remainder of the section).

The culms of *C. saximontana* (Fig. 3*f*), *C. backii* (Fig. 3*g*), and *C. juniperorum* (Figs. 3*c* and 3*d*) were distinguished by epidermal papillae. The papillae of *C. juniperorum*, however, were sparsely distributed and poorly developed by comparison with those on the culms of *C. saximontana* and *C. backii*. In *C. backii*, these papillae were confined to the apices of the wings, whereas in *C. saximontana* they were ubiquitous and often formed epistomatal cavities similar to those on its leaves (Fig. 3*f*).

Leaf epidermal surfaces

Epidermal surfaces were distinguished by distinct bulliform cells on the adaxial surface of the keel and by the presence of large rectangular cells in intercostal regions (Figs. 4*a* and 4*b*). The anticlinal cell walls of all species were highly sinuous, with the apex of the bends being thickened and often nodular in appearance (Fig. 4*a*). This was particularly pronounced in those cells immediately adjacent to stomata.

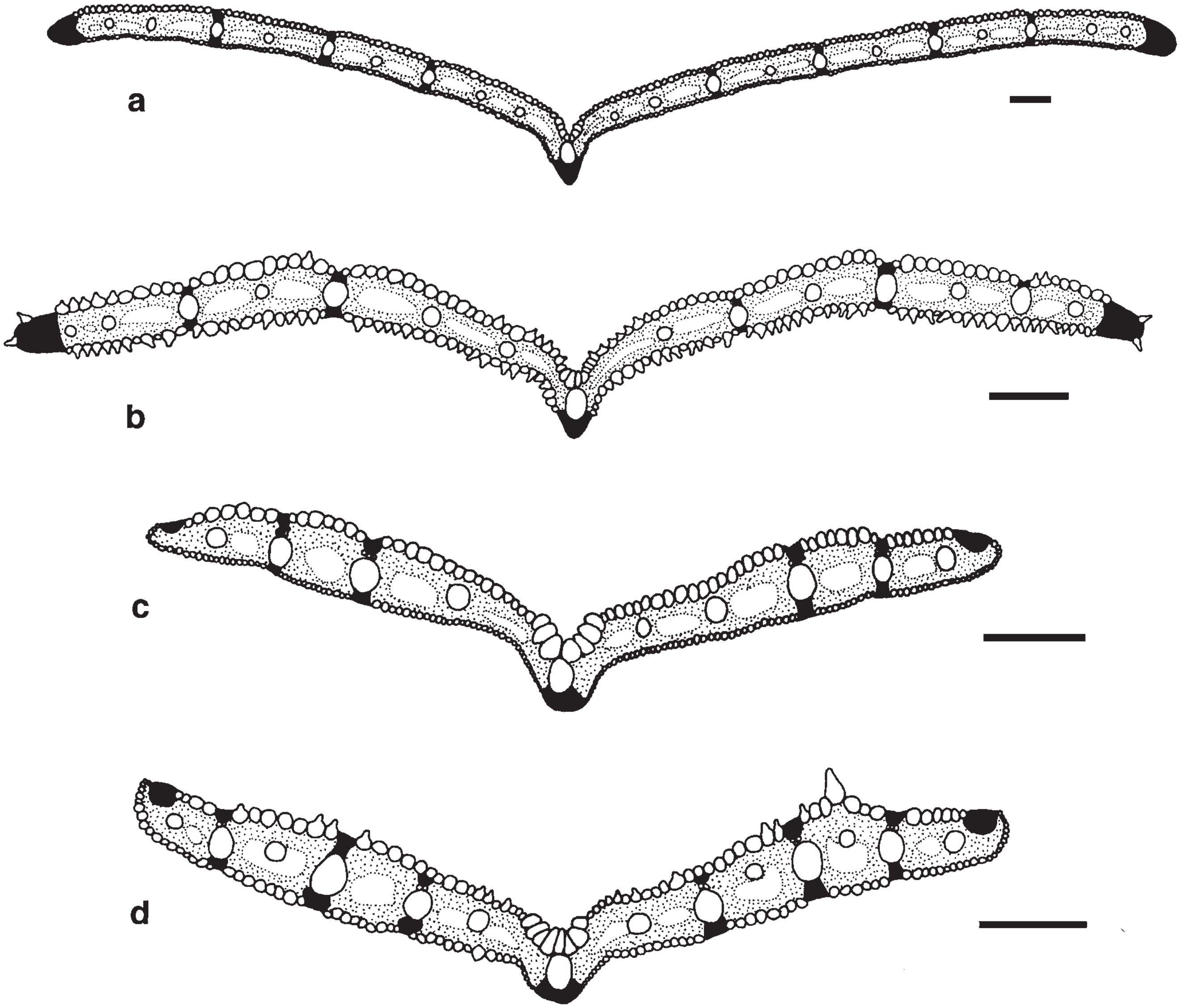
Conical silica bodies were often present in the small, square-like cells overlying the sclerenchyma of the girders, margins, and keel. Over girders, these cells were arranged in one to three longitudinal rows with each cell containing a single file of one to three (occasionally four, normally two) silica bodies (Fig. 4*a*). The only exception to this characteristic was in *C. willdenowii*, where as many as six silica bodies were arranged in two rows per cell on the abaxial surface. The silica bodies of this species were also unusual in that they possessed satellites, a feature that was also present in the silica bodies of its achenes (see below). At the leaf margin, these cells were usually found in three discontinuous rows (five in *C. latebracteata*) and often contained fewer silica bodies (one or two) than the cells overlying girders. In general, the number of cells occupied by silica bodies was directly correlated with the degree of sclerification.

The stomata in the section were found in numerous longitudinal rows in the intercostal region of abaxial surfaces (hypostomaty; Fig. 4*a*). The stomata in these rows may be separated by one to several intercostal cells; they were typically paracytic, and with the exception of two species (*C. jamesii* and *C. latebracteata*; orbicular to suborbicular), they were elliptical in outline. In all species examined, the intercostal cells adjacent to the stomata appeared to have grown slightly overtop of subsidiary cells. In some highly papillate individuals of *C. saximontana* (see above), an epistomatal cavity was formed by the arching of papillae (Fig. 4*a*).

The most distinct differences among taxa were observed in the presence or absence of papillae and prickle hairs on the surfaces and at the margins of the leaves. All prickle hairs (Fig. 4*b*) on the leaf pointed in an antrorse direction and were generally more consistent in their appearance than were papillae. At the margin, well-developed prickle hairs were seen in varying density in all species, except *C. latebracteata*. The leaf margin of this species was characterized by a tightly crenulate border of low papillae. Three species (*C. jamesii*, *C. basiantha*, and *C. superata*) displayed prickle hairs at the margin but no papillae. All specimens of *C. saximontana* had marginal prickle hairs and papillae except one (*Naczi 3372 & Thieret*, WIN), which was highly papillose and lacked prickle hairs.

On the surfaces of the leaf, papillae and prickle hairs were best developed on and close to the bulliform cells at the keel and around the small, square-like epidermal cells overlying girders (Fig. 4*b*). Three taxa (*C. saximontana, C. latebracteata, C. willdenowii*) often displayed papillae on the adaxial surfaces of their leaves. Papillae were also seen adaxially in *C. juniperorum* and *C. superata*, but their presence was rare. On the abaxial surface, papillae were seen in most samples of *C. willdenowii*, *C. saximontana*, and *C. juniperorum*. Three species (*C. willdenowii*, *C. juniperorum*, and *C. basiantha*) possessed prickle hairs on their adaxial surfaces. *Carex basiantha* possessed prickle hairs but no papillae, whereas *C. backii* and *C. jamesii* were the only two

Fig. 1. Cross sections of leaves. (*a*) *Carex latebracteata* (*Naczi 3948 & Ford*, WIN). (*b*) *Carex saximontana* (*Ford 9507 & Starr*, WIN). (*c*) *Carex jamesii* (*Naczi 3923 & Ford*, WIN). (*d*) *Carex juniperorum* (*Naczi 3878*, WIN). Scale bars to the right of figures = 0.25 mm. Darkened areas are sclerenchyma, stippled areas are chlorenchyma, stipple-bordered ellipses are air cavities, and continuous circles between upper and lower surfaces are vascular bundles.



species in the section to show neither papillae nor prickle hairs on their surfaces.

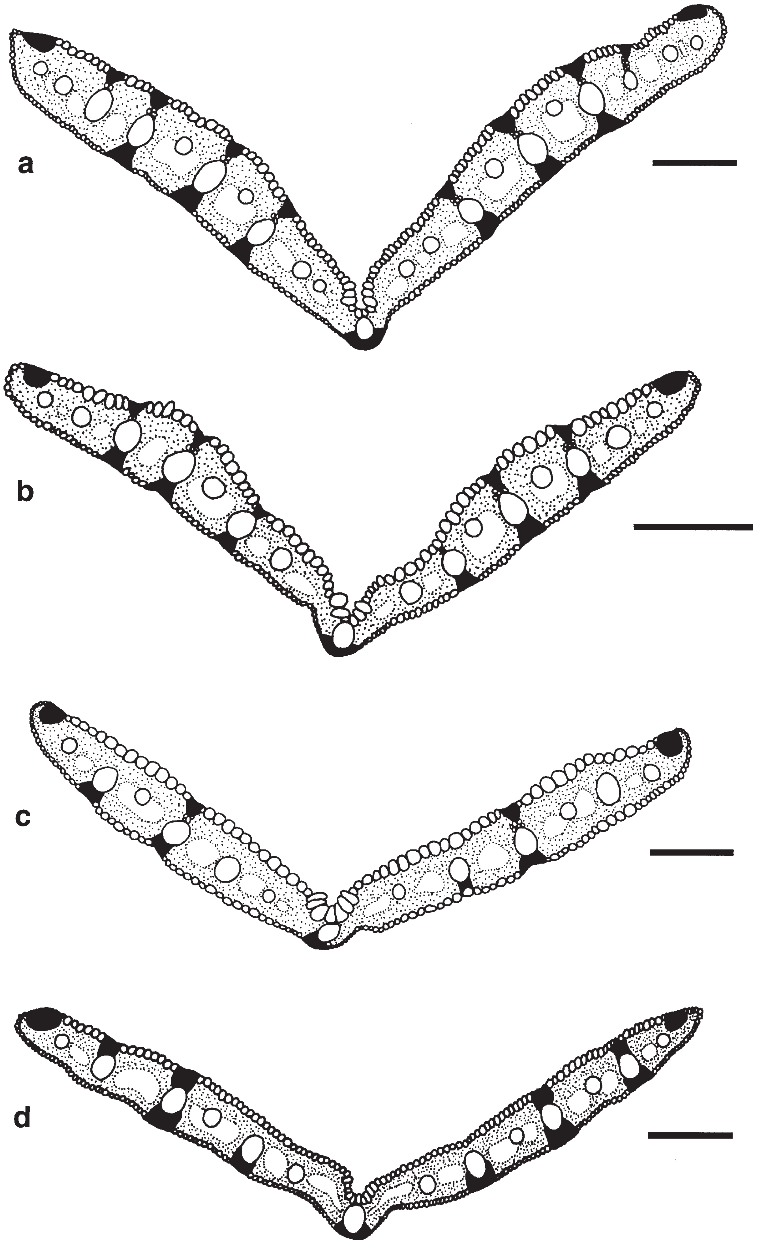
Silica bodies (micromorphology)

Silica bodies in section *Phyllostachys* were very similar in morphology and not unlike those seen in other *Carex* sections or cyperaceous genera. All members possessed a single, acute, conical central body that arose from the middle of either a convex or concave silica platform. The central body was always smooth and typically mucronate. All species possessed epidermal cell walls that were linear, typically six-sided, and isodiametric, although irregular cells and cells with five or seven sides were not uncommon. No significant micromorphological variations were observed within individuals.

The most notable differences among species were seen in the shape and relief of the silica platform. Based on these characters the section can be divided into two principal groups distinguished by platform margins that are either concave (*C. backii* and *C. saximontana*; Figs. 5*a* and 5*b*) or convex (*C. basiantha*, *C. juniperorum*, *C. jamesii*, *C. latebracteata*, *C. superata*, and *C. willdenowii*; Figs. 5*c*–5*f* and 6*a*–6*f*).

The concave group is only represented by the morphologically proximate species pair of *C. backii* and *C. saximontana*. Both these species exhibited concave silica platforms whose margins were appressed to the platforms of adjacent cells (Figs. 5*a* and 5*b*). Character differences between these two species were minimal and were confined to differences of degree, not character states. Some infraspecific variation was noted in *C. saximontana*. Individual achenes sampled from British Columbia (*Calder 10729 & Savile*, DAO) possessed considerably deeper silica platforms than those sampled from Minnesota (*Moore 19653 & Huff*, DAO) and North Dakota (*Stevens s.n.*, DAO; Fig. 5*b*). This

Fig. 2. Cross sections of leaves. (*a*) *Carex superata* (*Naczi 3993 & Ford*, WIN). (*b*) *Carex basiantha* (*Naczi 3954 & Ford*, WIN). (*c*) *Carex willdenowii* (*Naczi 3924 & Ford*, WIN). (*d*) *Carex backii* (*Ford 94119 et al.*, WIN). Scale bars to the right of figures = 0.25 mm. Darkened areas are sclerenchyma, stippled areas are chlorenchyma, stipple-bordered ellipses are air cavities, and continuous circles between upper and lower surfaces are vascular bundles.

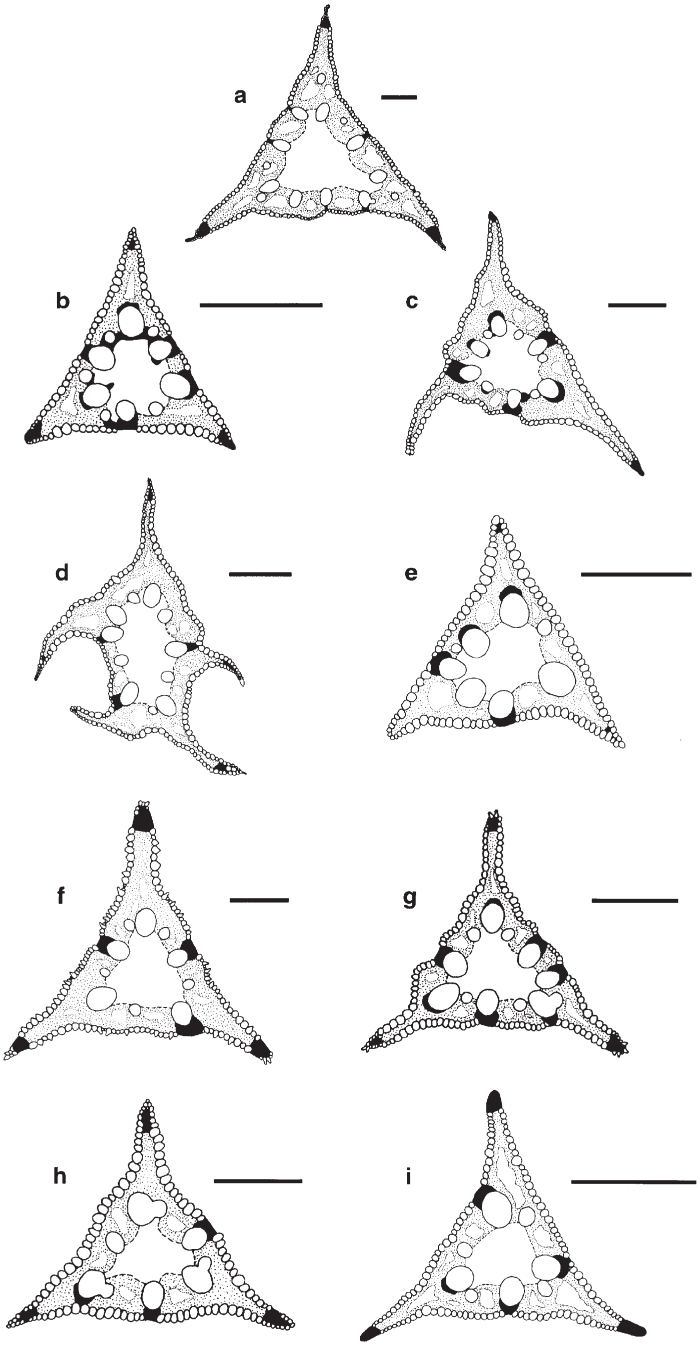


quality was in contrast to *C. backii*, where specimens examined from its eastern limits in New Brunswick (*Dore 45.198 & Gorham*, DAO) showed no significant differences in structure or size compared with specimens sampled from its western limits in British Columbia (Calder 17022 et al., DAO; Fig. 5*a*).

Among the species with convex margins, central platform characters distinguished two species pairs (*C. juniperorum* and *C. jamesii*, *C. basiantha* and *C. superata*) and the informal group known as the *C. willdenowii* complex (*C. basiantha*, *C. superata*, and *C. willdenowii* s.s.; Naczi et al. 1998).

The species pair of *C. juniperorum* and *C. jamesii* was characterized by tall, acute to abruptly acuminate central bodies surrounded by a trough created by a thickened ridge at the margin (Figs. 5*c* and 5*d*). Their platforms were tightly appressed, and the silica bodies were often arched (most pronounced in *C. jamesii*). As with *C. backii* and *C. saximontana*, the micromorphology of one species (*C. juniperorum*) was very consistent over its entire range, whereas the other (*C. jamesii*) was variable. Variation in *C. jamesii* was significant in the degree of ridge and trough development. This character varied from a distinct nodular

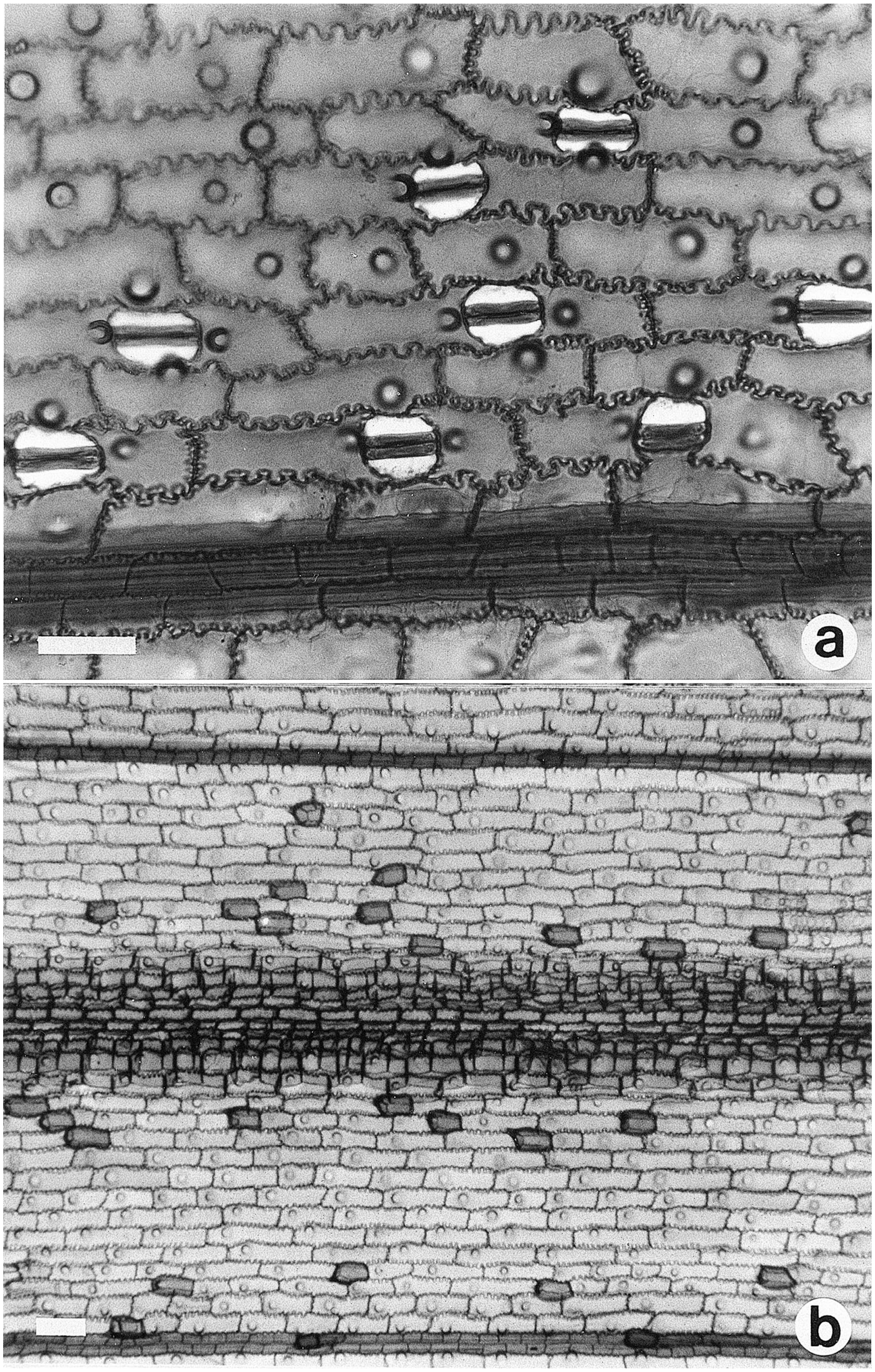
Fig. 3. Cross sections of culms. (*a*) *Carex latebracteata* (*Naczi 3952 & Ford*, WIN). (*b*) *Carex superata* (*Naczi 3993 & Ford*). (*c*) *Carex juniperorum*, Ontario (*Catling 9102*, WIN). (*d*) *Carex juniperorum*, Kentucky (*Naczi 3890*, WIN). (*e*) *Carex basiantha* (*Naczi 3965 & Ford*, WIN). (*f*) *Carex saximontana* (*Ford 9547 & Starr*, WIN). (*g*) *Carex backii* (*Ball s.n.*, WIN). (*h*) *Carex willdenowii* (*Naczi 3924 & Ford*, WIN). (*i*) *Carex jamesii* (*Naczi 3939 & Ford*, WIN). Scale bars to the right of figures represent 0.25 mm. Darkened areas are sclerenchyma, stippled areas are chlorenchyma, stipple-bordered ellipses are air cavities, and continuous circles between upper and lower surfaces are vascular bundles. The broken line separates chlorenchyma from the spongy central ground tissue.



embankment with a deep trough (Fig. 5*d*) to a low, poorly developed lip (Figs. 5*e* and 5*f*) with a shallow trough.

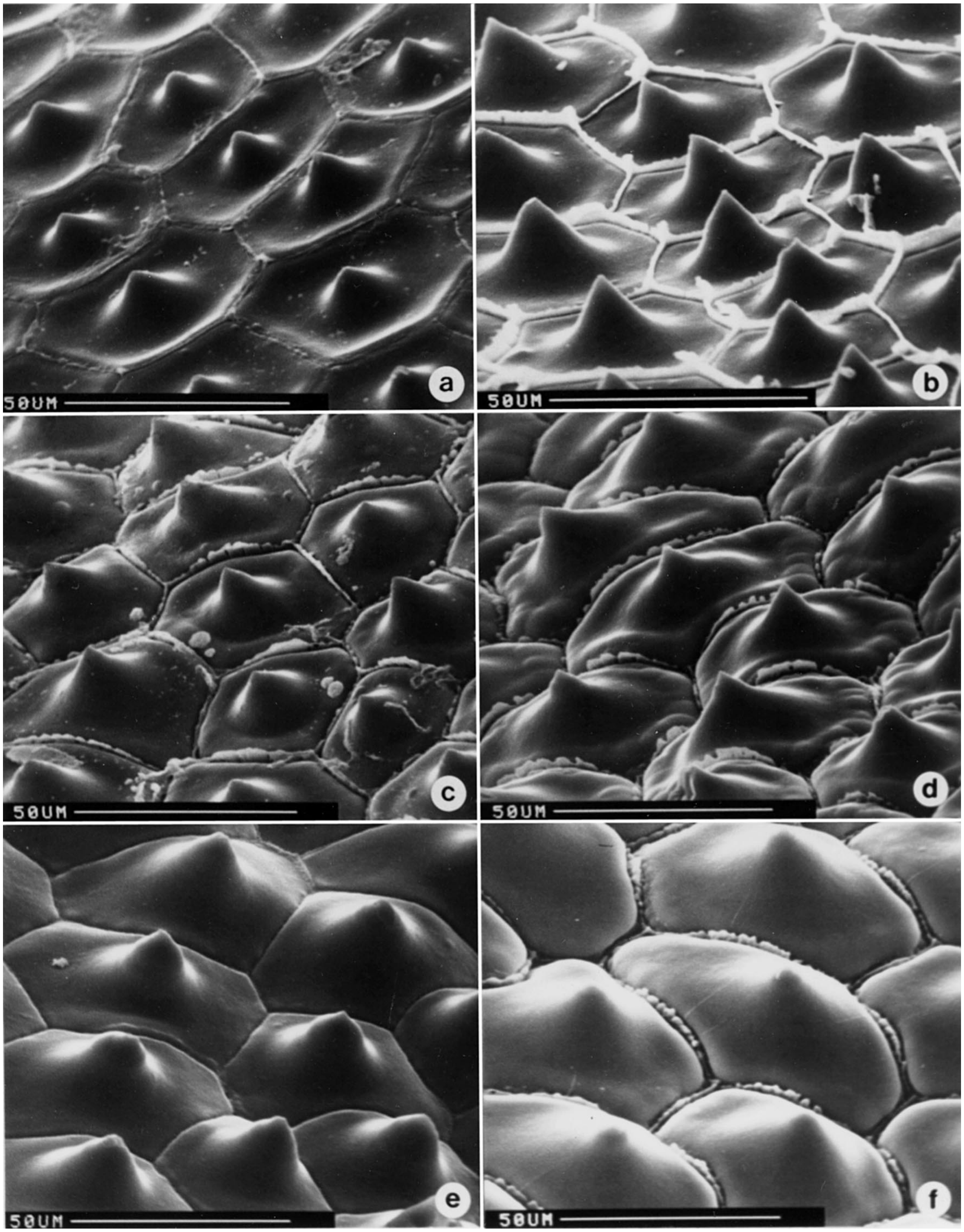
The species pair of *C. basiantha* and *C. superata* was recognized by distinctly raised silica platforms, small conical central bodies, and ornamented silica platforms. This ornamentation was particularly evident in *C. basiantha* where the platform, except for the central body, was ruminate in texture (Figs. 6*a* and 6*b*). In contrast, only small, weakly rugulose to bulbate peripheral areas were present on the platform of *C. superata* (Figs. 6*c* and 6*d*). The overall shape of the platform also differed. In *C. basiantha* a plateau was present, whereas in *C. superata* the platform continually rose until it reached the base of the central body (cf. Figs. 6*a* and 6*c*). Some infraspecific variation was detected in both

Fig. 4. Leaf epidermal surfaces. (*a*) *Carex saximontana*, abaxial surface (*Ford 9507 & Starr*, WIN). (*a*) *Carex willdenowii*, adaxial surface (*Naczi 4287*, WIN). Scale bars = 100 µm.



species. Low, poorly developed nodules were observed on a specimen of *C. superata* from Tennessee (*Kral 42454b*, MICH; Fig. 6*d*), whereas another from Mississippi (*Naczi 4013 et al.*, WIN) displayed similarly textured platforms to *C. basiantha* but only in a few epidermal cells. A comparable level of variation was seen in *C. basiantha*. One specimen from South Carolina (*Hill 19477*, MICH) possessed rounded as opposed to acute central bodies, whereas another (*Naczi 3938*, WIN; Fig. 6*b*) lacked the distinctly convex central platforms characteristic of the *C. willdenowii* complex as

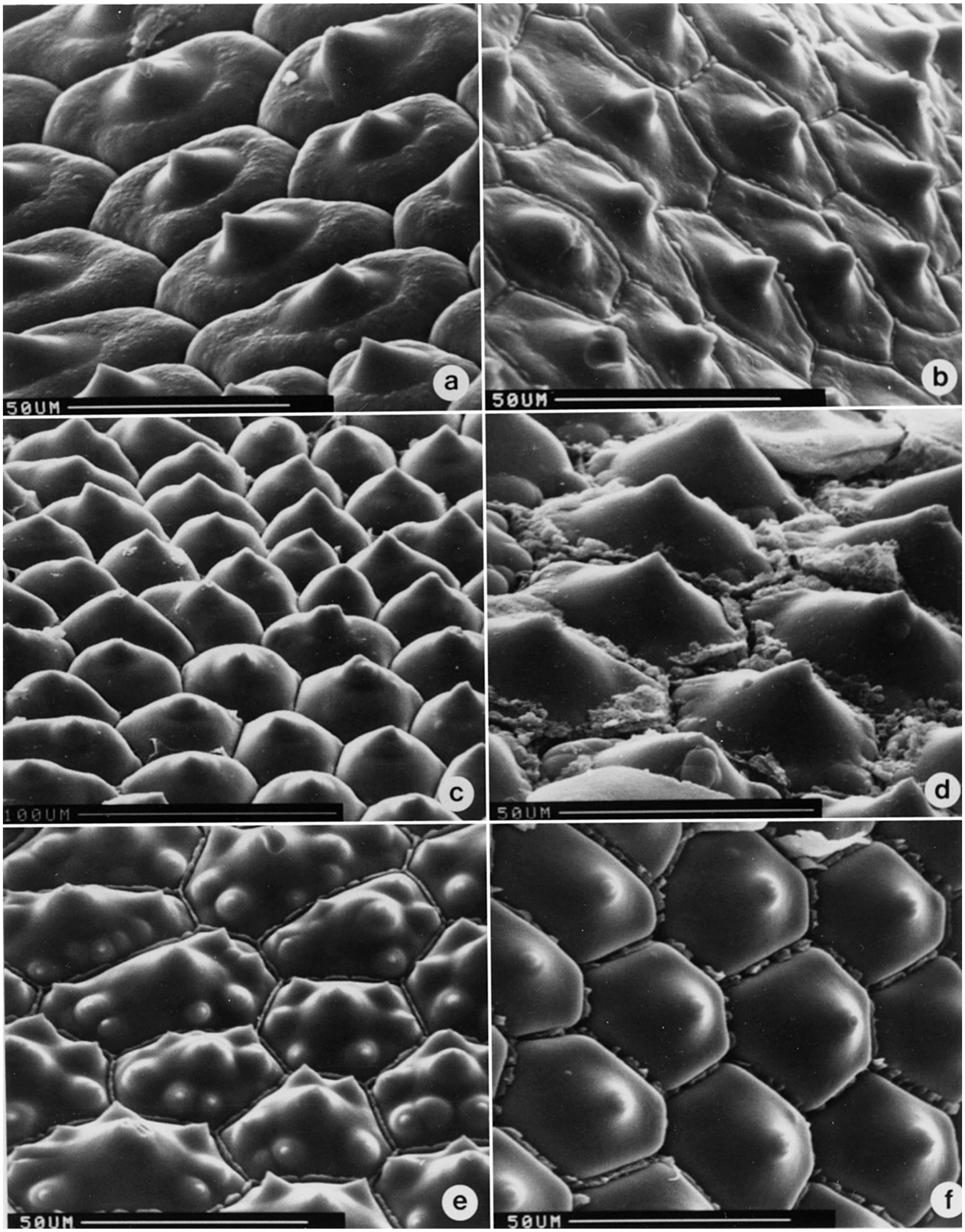
Fig. 5. Scanning electron micrographs of silica deposits in achene epidermal cells of *Carex* spp. (*a*) *Carex backii* (*Calder 17022 et al.*, DAO). (*b*) *Carex saximontana* (*Stevens s.n.*, DAO). (*c*) *Carex juniperorum* (*Reznicek 8742 et al.*, MICH). (*d*) *Carex jamesii*, Virginia (*Wieboldt 5982*, MICH). (*e*) *Carex jamesii*, Indiana (*Deam 12, 858*, MICH). (*f*) *Carex jamesii*, Iowa (*Wilson 5175*, MICH).



a whole (see below). The rugulose portion of the central plateau in *C. basiantha* also showed some variation in the area it covered. Nonetheless, the main characters of these two species were consistent enough that the silica bodies of any one specimen could be easily identified and distinguished from the silica bodies of any other species in the section.

Carex willdenowii had the most striking silica bodies in the section because of the presence of conical satellites (5–10; Fig. 6*e*). These satellites were similar in morphology to the central body and angled away from the main axis of the cell. Like *C. basiantha* and *C. superata*, the central platform of *C. willdenowii* was distinctly convex (Fig. 6*e*).

Fig. 6. Scanning electron micrographs of silica deposits in achene epidermal cells of *Carex* spp. (*a*) *Carex basiantha*, Louisiana (*Naczi 3987 & Ford*, WIN). (*b*) *Carex basiantha*, Arkansas (*Naczi 3938*, WIN). (*c*) *Carex superata*, Alabama (*Naczi 3103*, WIN). (*d*) *Carex superata*, Tennessee (*Kral 42454b*, MICH). (*e*) *Carex willdenowii* (*Cusick 29, 595*, MICH). (*f*) *Carex latebracteata* (*Naczi 3953 & Ford*, WIN).



In contrast, *Carex latebracteata* was unique in its possession of silica bodies with large, lightly sloping central bodies located on convex platforms whose margins were not appressed to the platforms of adjacent cells (Fig. 6*f*). Its cells were more regular in size and shape than other species, and unlike the remainder of the section, its long, outer periclinal cell walls were persistent despite repeated acetelyzing and sonication treatments. This trait appeared to be unrelated to

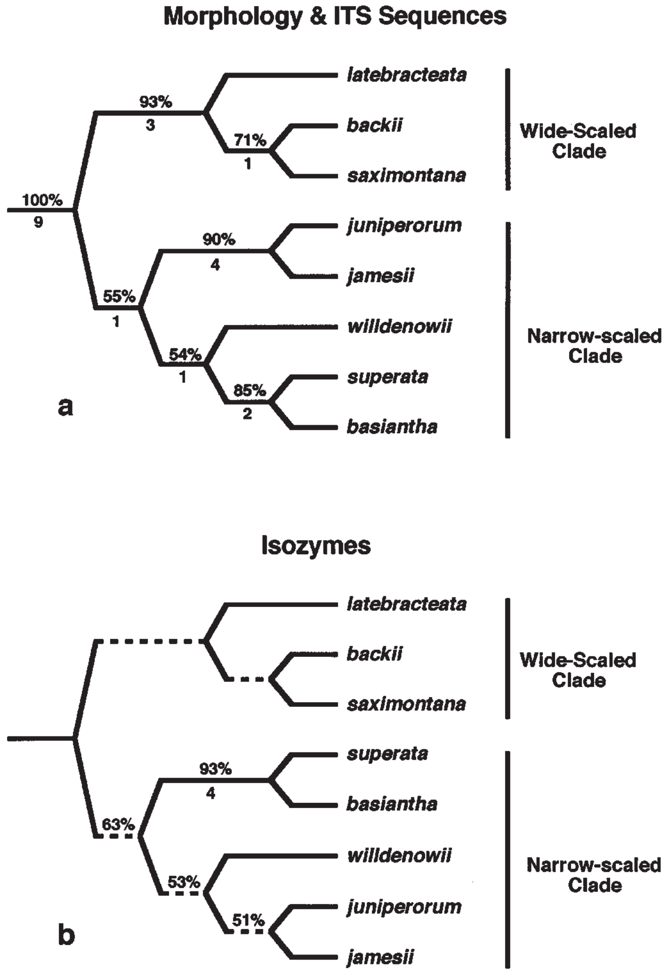


Fig. 7. Phylogenetic analyses of *Carex* section *Phyllostachys*. (*a*) The single most parsimonious tree obtained using morphology and ITS sequences. The tree is 182 steps long with a consistency index (CI) of 0.86 and a retention index (RI) of 0.73 (Starr 1997). Numbers above branches are bootstrap values, while numbers below branches are decay values. Sections *Firmiculmes* and *Filifoliae* were used as outgroups as suggested by the analyses of Starr (1997) and Starr et al. (1999). (*b*) The 50% majority rule tree of five most parsimonious trees based on isozyme data. Trees are 56 steps long with a CI of 0.86 and an RI of 0.49 (Ford et al. 1998*a*). Numbers above branches are bootstrap values, while numbers below branches are decay values. Branches that collapse in the strict consensus tree are broken. Individual alleles were coded as present or absent. The wide-scaled clade was used as the outgroup.

the age of the achene and was unique in the section. The silica bodies of *C. latebracteata* could not be easily aligned with other species with convex margins.

Discussion

Taxonomic trends

Anatomical and micromorphological data support the recognition of eight species in *Carex* section *Phyllostachys*. In particular, the data strongly support the separation of the critical species pair of *C. backii* and *C. saximontana* and the recognition of three species within the *C. willdenowii* complex.

Leaf and culm anatomy clearly separate *C. saximontana* from *C. backii*. The tendency for the leaf margins to be completely sclerified, glaucous induments (Starr 1997), thin, revolute leaves, and the distribution of papillae on both surfaces of the leaf and along the entire surface of the culm are consistent features that *C. saximontana* does not share with *C. backii*. In fact, anatomically, *C. saximontana* is far closer to *C. latebracteata* than it is to *C. backii*.

Anatomical and silica body characters strongly support previous morphological (Naczi et al. 1998) and isozyme studies (Ford et al. 1998*c*) that have recognized three species within *C. willdenowii* s.l. (i.e., *C. willdenowii* s.s., *C. basiantha*, and *C. superata*). Moreover, this species complex is a clear example of how useful epidermal (e.g., Le Cohu 1970) and silica body characters (Wujek and Menapace 1986) can be for circumscribing species within critical groups. The three taxa recognized by Naczi et al. (1998) differ markedly in the distribution of papillae and prickle hairs on their leaves and in the micromorphology of their silica bodies. *Carex willdenowii* s.s. tends to have papillae on both surfaces of its leaf and prickle hairs adaxially, whereas *C. superata* lacks prickle hairs and only rarely has adaxial papillae. *Carex basiantha* lacks papillae but possesses adaxial prickle hairs. Silica body variation is even more striking among these species. Whereas the silica platform in *C. basiantha* is ruminate, it is smooth in *C. superata*, and neither taxon possesses the distinctive satellite bodies of *C. willdenowii* s.s. Culm anatomy provides yet another distinguishing character. Whereas the culm sclerification of *C. willdenowii* s.s. is typical of the majority of the species in the section, the culms of *C. basiantha* are weakly sclerified, and those of *C. superata* are highly sclerified. This may explain why *C. willdenowii* s.s. has an intermediate habit to the long, widely spreading culms of *C. basiantha* and the short, stiff culms of *C. superata* (see Naczi et al. 1998, Fig. 6).

The remaining three species in the section (*C. juniperorum*, *C. jamesii*, and *C. latebracteata*) also possess interesting anatomical features that are worth noting. For example, the short, often asymmetric, three- to five-winged culm of *C. juniperorum* is highly unusual and possibly unique in *Carex*. The peculiar shape and wing number of these culms could be a phenotypic response to their tight investment in the leaf sheaths of the pseudoculm; however, these characters are not found in the culms of *C. superata*, which is similarly short stemmed, suggesting that they might be genetically controlled. *Carex latebracteata* is unique in possessing a culm with minor vascular bundles completely within chlorenchyma and in possessing a tightly crenulate leaf margin composed of low papillae. In contrast to the above-named species, *C. jamesii* did not possess any distinguishing anatomical features. It was, however, the only species to show significant variation in its silica bodies, which is consistent with the high levels of genetic and morphological variability observed within the species as a whole (Ford et al. 1998*b*).

Phylogenetic implications

A phylogenetic analysis of *Carex* section *Phyllostachys* based on morphology and ITS sequences suggested that the section could be divided into two principal clades: (*i*) a "wide-scaled" clade comprised of *C. latebracteata* and its sister taxa *C. backii* and *C. saximontana* and (*ii*) a "narrow-scaled" clade composed of two major groups, *C. jamesii* and *C. juniperorum* and the *C. willdenowii* complex (details in Starr 1997; Fig. 7*a*). A cladistic analysis of isozyme data in the section produced trees that were largely in agreement with the above analysis; however, support for the hypotheses was poor, and the trees suggested that the *C. willdenowii* complex was unnatural (cf. Figs. 7*a* and 7*b*; Ford et al. 1998*a*). Mindful that our assessment is phenetic, the present silica body data would appear to support the *C. willdenowii* complex as natural and to define all three species pairs previously identified in both the morphology – ITS sequence analysis and the isozyme analysis. Only in the wider grouping of *C. latebracteata* with members of the narrow-scaled clade do we see a conflict with the above phylogenetic analyses. In contrast, relationships inferred from anatomical leaf, culm, and epidermal characters appear to conflict significantly with silica body data and with previous cladistic analyses. The wider relevance of these results is discussed below.

Although the congruence between our micromorphological data and previous phylogenetic studies suggests that silica bodies are good indicators of evolutionary relationship in the *Phyllostachys*, their general use for inferring relationships in *Carex* is controversial. While many studies have shown that these characters can be used to circumscribe sections (e.g., Walter 1975; Toivonen and Timonen 1976; Menapace et al. 1986; Menapace and Wujek 1987) and species (Wujek and Menapace 1986), others have found no distinguishing sectional characters (Waterway 1990; Naczi 1992; this study), a lack of differences among seemingly distant species (Waterway 1990; Dan and Hoshino 1994), and marked intraspecific variation (Rettig 1990; Salo et al. 1994). Several studies have now noted similarities in silica bodies between distantly related sections in *Carex* and even between *Carex* and other cyperaceous genera (Rettig 1986; Waterway 1990; Salo et al. 1994). In the present study, for example, silica bodies similar to *C. backii*'s (Fig. 5*a*) are seen in several disparate *Carex* sections (cf. Le Cohu 1973; Walter 1975; Hoshino 1984; Waterway 1990), whereas those of *C. latebracteata* (Fig. 6*f*) and *C. jamesii* (Fig. 5*d*) appear similar to the silica bodies seen in certain species of *Scirpus* and *Eriophorum* (cf. Tucker and Miller 1990). Observations such as these have prompted some authors to suggest that silica body characters are too homoplastic to be reliable indicators of evolutionary relationship (Rettig 1986; Waterway 1990). While this may often be the case, this study and others involving closely related taxa have found some correspondence between morphological and silica body variation. For example, the marked intraspecific variation and wide overlap in characters observed in the silica bodies of the *Carex flava* complex (section *Ceratocystis* Dumort) are also seen in its morphology and anatomy (Salo et al. 1994). Species grouped on the basis of their silica bodies often correspond to natural groupings on the basis of morphology (e.g., Walter 1975; Menapace et al. 1986; Starr 1997) and other types of data such as flavonoids (Toivonen and Timonen 1976), DNA sequences (Starr et al. 1999), and isozymes (Waterway 1990; Ford et al. 1998*a*). Furthermore, Naczi's (1992) cladistic analysis of section *Griseae* (18 species) demonstrates that silica body characters can provide synapomorphic support for some small clades (a maximum of four species). Considered in full, the above studies suggest that silica body characters are good indicators of relationship but only within clearly defined groups of closely related species.

Unfortunately, the use of silica bodies in cladistic analyses is still complicated by a poor understanding of the effects of the environment (e.g., soil Si availability) and development (e.g., maturity of achenes, genetic basis of characters) on structure, by the difficulties of defining discrete character states, and by the small number of potential characters. Autapomorphies, such as the satellite bodies of *C. willdenowii*, are relatively common; however, potentially informative characters with discrete states, of which only the shape of the silica platform (concave vs. convex) appears to qualify in this study, are not. Considering these caveats, silica bodies are probably best used for circumscribing species in critical groups (e.g., *C. willdenowii* complex, see above) and as external data sets (e.g., Crins and Ball 1988), which can be used as an independent evaluation of relationships inferred from more conserved and abundant character sources such as morphology (e.g., Crins and Ball 1988; Crins 1990; Naczi 1992) or DNA sequences (Starr 1997; Starr et al. 1999).

Although micromorphological characters suggest groups that are congruent with those expected from the cladistic analysis of morphology, ITS sequences, and isozymes, groupings based on anatomical data sets (i.e., leaf, culm, and leaf epidermal characters) are in conflict with those derived from other data sets. This would seem to indicate that stasis or homoplasy is high in anatomical characters which is consistent with the results of other studies (e.g., Akiyama 1942; Standley 1987, 1990; Ford and Ball 1992). Anatomical differences among species of *Phyllostachys* are few and are mostly confined to the presence or absence of prickle hairs and papillae. If we consider papillae and prickle hairs to be derived characters (Standley 1990), a wide number of disparate groupings are obtained. The frequent presence of papillae on the adaxial surface of the leaves of *C. saximontana*, *C. latebracteata*, and *C. willdenowii* and rarely on *C. juniperorum* and *C. superata* might suggest that these five taxa should form a group. However, only *C. saximontana*, *C. juniperorum*, and *C. willdenowii* have papillae on both leaf surfaces, and although a relationship between *C. willdenowii* and *C. juniperorum* might appear to be further supported by the presence of adaxial prickle hairs, they share this trait with *C. basiantha*, a species that entirely lacks papillae. Yet another group is suggested by the presence of papillae on the culms of *C. saximontana*, *C. backii*, and *C. juniperorum*. Furthermore, qualitative leaf characters such as the wide, glaucous (Starr 1997), revolute leaf with completely sclerified margins of *C. latebracteata* and *C. saximontana* would suggest that these two species are most closely related; however, morphological characters (Mackenzie 1906; Starr 1997), ITS sequence data (Starr 1997; Starr et al. 1999), and isozyme analyses (Ford et al. 1998*a*, 1998*b*) strongly suggest that *C. saximontana* is closest to *C. backii*.

Even though anatomical (i.e., leaf, culm, epidermis) characters have been of enormous value in distinguishing morphologically difficult species pairs (e.g., *Carex vesicaria* L. and *Carex rostrata* Stokes; Le Cohu 1970; *Carex rotundata* and *Carex membranacea*, Ford and Ball 1992), characters are often few, difficult to define (see papillae examples above), and appear to exhibit high levels of homoplasy (Standley 1990). These problems make anatomical characters difficult to use in phylogenetic studies and brings into question their ability to accurately reflect phylogenetic relationships. Shepherd (1976) and Standley (1990) have both found that, although some relationship between anatomical characters and present morphological classifications appears to exist, when anatomical characters are used alone, they produce groups that are clearly unnatural. Some of these incongruities between morphological and anatomical trends could be explained by circumscriptional problems; however, if this were the only reason, we would not have expected to see the same types of inconsistencies in a small, clearly marked section like the *Phyllostachys* as we do in larger groups (cf. Standley 1987, 1990). Our data suggest that anatomical leaf, culm, and epidermal characters are effective indicators of species limits, but owing to a lack of easily defined qualitative characters and high levels of homoplasy or stasis, their role in future phylogenetic studies below the sectional level in *Carex* may be limited. Future studies may find that the anatomy of reproductive structures is more phylogenetically informative (see Naczi 1992).

Conclusions

Anatomical and fruit silica body characters support the recognition of eight species within *Carex* section *Phyllostachys*. Leaf and culm anatomy clearly separate the close species pair of *C. backii* and *C. saximontana*, and they provide unique characters that distinguish *C. latebracteata* and *C. juniperorum*. Anatomical and silica body characters strongly support the recognition of three species within the *C. willdenowii* complex (see Naczi et al. 1998; Ford et al. 1998*c*). Although unique characters were lacking in *C. jamesii*, infraspecific variation in its silica bodies was consistent with the high levels of genetic and morphological variation previously detected (Ford et al. 1998*b*).

All of the species pairs suggested by silica body characters, and the alignment of *C. willdenowii* with *C. basiantha* and *C. superata*, are consistent with previous phylogenetic analyses based on morphological, DNA sequence, and isozyme data. The difficulties associated with small character numbers, a lack of discrete character states, and the unknown effects of the environment and development on structure suggest, however, that silica body characters are best used for circumscribing critical groups and as external data sets for assessing phylogenetic hypotheses derived from more conserved characters such as morphology or DNA sequence data.

Relationships inferred from vegetative anatomy conflict significantly with previous cladistic analyses and with silica body data, suggesting that the contribution of vegetative anatomy to future phylogenetic reconstructions below the sectional level in *Carex* may be limited.

Despite the general findings of this study, the disparate opinions regarding the usefulness of anatomical and silica body characters suggests that their utility is probably taxon dependant. Given the vastness, complexity, and poor understanding of phylogeny and character evolution in *Carex*, no phylogenetic or taxonomic study can afford to dismiss these or any other characters a priori.

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Appendix 1

Collection data for populations of *Carex* section *Phyllostachys* for which leaf cross sections were examined. Vouchers are deposited at KNK and WIN unless otherwise noted. Herbarium acronyms follow Holmgren et al. (1990).

Carex backii
CANADA: MANITOBA: Hwy. 308, 5 km S of Forestry Rd. 5, 13 June 1994, *Ford 94119 et al*.; Delta Marsh, University of Manitoba Field Station, 12 July 1994, *Ford 94191 & Starr* (3 samples); ONTARIO: Niagara Regional Mun., North Grimsby Twp., Beamer Conservation Area, 15 June 1994, *Ball s.n.* (3 samples); Simcoe Co., Vespra Twp., 5 mi. NW of Barrie, 26 July 1981, *Reznicek & Reznicek 6364*. (MICH); Victoria Co., Carden Twp. Mun., Carden Alvar, rocky woods 5.3 km S of Uphill, 26 May 1994, *Oldham 16032*. (TRTE).

Carex basiantha
U.S.A.: ALABAMA: Butler Co., ca. 0.5 mi N of Oaky Streak, 23 May 1994, *Naczi 3991 & Ford*.; ARKANSAS: Scott Co., ca. 2 mi. N of Y City, 20 May 1994, *Naczi 3938 & Ford*; LOUISIANA: West Feliciana Parish, along W side of route 61, just S of St. Francis Hotel, 23 May 1994, *Naczi 3987 & Ford*; OKLAHOMA: McCurtain Co., ca. 4 mi. N of Idabel, 21 May 1994, *Naczi 3954 & Ford*; TEXAS: Jasper Co., ca. 12 mi. W of Jasper, 22 May 1994, *Naczi 3965 & Ford* (2 samples).

Carex jamesii
CANADA: ONTARIO: Essex Co., Anderdon Twp., 5 km NE of Amherstburg, 22 May 1994, *Ball 940526*; Niagara Regional Mun., Louth Twp., Twenty Mile Creek, Jordan, 13 June 1979, *Ball 79039 PWB*. (TRTE).; Essex Co., Pelee Island, 9 June 1994, *Oldham 16117* (2 samples); Waterloo Co., Wilmot Twp., 8 km W of New Dundee on the Nith River, 3 June 1982, *Ball 82074 PWB*. (TRTE); U.S.A.: ARKANSAS, Franklin Co., ca. 1 mi. N of Cecil, Citadel Bluff Army Corps of Engineers Park, 19 May 1994, *Naczi 3923 & Ford*; Newton Co., ca. 3 mi NE of Boxley, Lost Valley Recreation Area of Buffalo National River, 19 May 1994, *Naczi 3917 & Ford*; Scott Co., ca. 2 mi. N of Y City, W of route 71 and S of Fourche La Fave River, 20 May 1994, *Naczi 3939 & Ford*; INDIANA. Grant Co., Taylor University Arboretum, SW edge of Upland, 17 May 1994, *Rothrock 3255*; Stellers Road, 1.3 mi. N of Matthews, 17 May 1994, *Rothrock 3254*; KENTUCKY: Campbell Co., Highland Heights, 10 May 1994, *Naczi 3826*; Mason Co.: ca. 2 air mi. W of Dover, along S side of route 8, 29 May 1994, *Naczi 4028 & Flynn*; MISSISSIPPI: DeSoto Co., ca. 2 mi. N of Walls, along E side of Rte. 61, 25 May 1994, *Naczi 4026 et al*.; VIRGINIA: Bath Co., ca. 0.4 mi. S of Healing Springs, along W side of Rte. 220, 23 June 1994, *Naczi 4482 & Thieret*.

Carex juniperorum
U.S.A.: KENTUCKY: Bath Co., ca. 5 air mi ESE of Owingsville, 16 May 1994, *Naczi 3890* (2 samples); Lewis Co., ca. 3.5 air mi. ESE of Trinity, 5 May 1994, *Naczi 3808 et al*. (2 samples); OHIO: Adams Co., ca. 3 air mi. NE of Peebles, 16 May 1994, *Naczi 3878*.

Carex latebracteata
U.S.A.: ARKANSAS: Howard Co., ca. 4 mi NW of Athens, 21 May 1994, *Naczi 3952 & Ford*; Polk Co., ca. 8 mi. E of Vandervoort, 20 May 1994, *Naczi 3948 & Ford* (2 samples); OKLAHOMA: McCurtain Co., ca. 10 road mi. N of Broken Bow, 21 May 1994, *Naczi 3953 & Ford*.

Carex saximontana
CANADA: MANITOBA: Treesbank, 300 m E of Prov. Rd. 530 where road crosses the Souris River, 9 June 1995, *Ford 9501 & Starr*; SASKATCHEWAN: Cypress Hills, ca. 6 km NW of Eastend, 11 June 1995, *Ford 9526 & Starr*; Besant Campground and Recreation Area, ca. 30 km W of Moose Jaw, 14 June 1995, *Ford 9547 & Starr*; U.S.A.: UTAH: Utah Co., Timpanogos National Monument parking area. Along highway 92 E of Alpine, 10 August 1993, *Naczi 3372 & Thieret*.

Carex superata
U.S.A.: ALABAMA: Butler Co.: ca. 0.5 mi. N of Oaky Streak, 23 May 1994, *Naczi 3990 & Ford*; Greenville, 3 mi. N of center of town along Rte. 263, 24 May 1994, *Naczi 3993 & Ford*; MISSISSIPPI: Tishomingo Co., ca. 10 mi N of Iuka, J. P. Coleman State Park, 25 May 1994, *Naczi 4013 et al*.

Carex willdenowii
U.S.A.: ARKANSAS: Garland Co., ca. 17 air mi. N of Hot Springs, Iron Springs Recreation Area of Ouachita National Forest, 19 May 1994, *Naczi 3924 & Ford*; KENTUCKY: Franklin Co., ca. 6.5 air mi. NW of Frankfort, 11 May 1994, *Naczi 3835 & Borne*; OHIO: Pike Co., 1.5 road mi. W of Buchanan, 16 May 1994, *Naczi 3887*; PENNSYLVANIA: Bradford Co., ca. 8 mi. SW of Towanda, along W side of Preacher Brook Road, 17 June 1994, *Naczi 4287 & Thieret*.

Appendix 2

Collection data for populations of *Carex* section *Phyllostachys* for which culm cross sections were examined. Vouchers are deposited at KNK and WIN unless otherwise noted. Herbarium acronyms follow Holmgren et al. (1990).

Carex backii
CANADA: MANITOBA: Delta Marsh, University of Manitoba Field Station, 12 July 1994, *Ford 94191 & Starr*; ONTARIO: Niagara Regional Mun., North Grimsby Twp., Beamer Conservation Area, 15 June 1994, *Ball s. n.*; Simcoe Co., Vespra Twp., 5 mi. NW of Barrie, 26 July 1981, *Reznicek & Reznicek 6364*. (MICH).

Carex basiantha
U.S.A.: ARKANSAS: Scott Co., ca. 2 mi. N of Y City, 20 May 1994, *Naczi 3938 & Ford*; OKLAHOMA: McCurtain Co., ca. 4 mi. N of Idabel, 21 May 1994, *Naczi 3954 & Ford*; TEXAS: Jasper Co., ca. 12 mi. W of Jasper, 22 May 1994, *Naczi 3965 & Ford* (2 samples).

Carex jamesii
CANADA: ONTARIO. Essex Co., Pelee Island, 9 June 1994, *Oldham 16117*; Niagara Regional Mun., Louth Twp., Twenty Mile Creek, Jordan, 13 June 1979, *Ball 79039 PWB*.

(TRTE); U.S.A.: ARKANSAS: Scott Co., ca. 2 mi. N of Y City, W of Rte. 71 and S of Fourche La Fave River, 20 May 1994, *Naczi 3939 & Ford*.

Carex juniperorum
CANADA: ONTARIO: Hastings Co., Tyendinaga Twp. 5.5 km NE of Shannonville, 11 June 1991, *P.M. Catling 9102*. (MICH); U.S.A.: KENTUCKY: Bath Co., ca. 5 air mi. ESE of Owingsville, 16 May 1994, *Naczi 3890*; Lewis Co., Hymes Knob, 1.25 mi. E of Trinity School, 7 May 1991, *A. A. Reznicek 8756, A.W. Cusick & Reznicek*. (MICH); OHIO: Adams Co., ca. 3 air mi. NE of Peebles, 16 May 1994, *Naczi 3878*.

Carex latebracteata
U.S.A.: ARKANSAS: Howard Co., ca. 4 mi. NW of Athens, 21 May 1994, *Naczi 3952 & Ford*; Polk Co., ca. 8 mi. E of Vandervoort, 20 May 1994, *Naczi 3948 & Ford*; OKLAHOMA: McCurtain Co., ca. 10 road mi. N of Broken Bow, 21 May 1994, *Naczi 3953 & Ford*.

Carex saximontana
CANADA: MANITOBA: Manitoba Wildlife Management Area, W side of Prov. Rd. 346 where road crosses Souris River, 9 June 1995, *Ford 9507 & Starr*; SASKATCHEWAN: Besant Campground and Recreation Area, ca. 30 km W of Moose Jaw, 14 June 1995, *Ford 9547 & Starr*; U.S.A.: UTAH: Utah Co., Timpanogos National Monument parking area. Along Hwy. 92 E of Alpine, 10 August 1993, *Naczi 3372 & Thieret*.

Carex superata
U.S.A.: ALABAMA: Butler Co., ca. 0.5 mi. N of Oaky Streak, 23 May 1994, *Naczi 3990 & Ford*; Greenville, 3 mi. N of center of town along Rte. 263, 24 May 1994, *Naczi 3993 & Ford*; MISSISSIPPI: Tishomingo Co., ca. 10 mi. N of Iuka, J.P. Coleman State Park, 25 May 1994, *Naczi 4013 et al*.

Carex willdenowii
U.S.A.: ARKANSAS: Garland Co., ca. 17 air mi. N of Hot Springs, Iron Springs Recreation Area of Ouachita National Forest, 19 May 1994, *Naczi 3924 & Ford*.; OHIO: Pike Co., 1.5 road mi. W of Buchanan, 16 May 1994, *Naczi 3887*; PENNSYLVANIA: Bradford Co., ca. 8 mi. SW of Towanda, along W side of Preacher Brook Road, 17 June 1994, *Naczi 4287 & Thieret*.

Appendix 3

Collection data for populations of *Carex* section *Phyllostachys* for which leaf epidermal surfaces were surveyed. Vouchers are deposited at KNK and WIN unless otherwise noted. Herbarium acronyms follow Holmgren et al. (1990).

Carex backii
CANADA: MANITOBA: Delta Marsh, University of Manitoba Field Station, 12 July 1994, *Ford 94191 & Starr*: ONTARIO: Niagara Regional Mun., North Grimsby Twp., Beamer Conservation Area, 15 June 1994, *Ball s. n.*; Victoria Co., Carden Twp. Mun., Carden Alvar, rocky woods 5.3 km S of Uphill, 26 May 1994, *Oldham 16032*. (TRTE).

Carex basiantha
U.S.A.: ALABAMA: Butler Co., ca. 0.5 mi. N of Oaky Streak, 23 May 1994, *Naczi 3991 & Ford*; OKLAHOMA: McCurtain Co., ca. 4 mi. N of Idabel, 21 May 1994, *Naczi 3954 & Ford*; TEXAS: Jasper Co., ca. 12 mi W of Jasper, 22 May 1994, *Naczi 3965 & Ford*.

Carex jamesii
CANADA: ONTARIO: Essex Co., Pelee Island, 9 June 1994, *Oldham 16117*; Niagara Regional Mun., Louth Twp., Twenty Mile Creek, Jordan, 13 June 1979, *Ball 79039 PWB*. (TRTE); U.S.A.: ARKANSAS: Franklin Co., ca. 1 mi. N of Cecil, Citadel Bluff Army Corps of Engineers Park, 19 May 1994, *Naczi 3923 & Ford*.

Carex juniperorum
U.S.A.: KENTUCKY: Bath Co.: ca. 5 air mi ESE of Owingsville, 16 May 1994, *Naczi 3890*; Lewis Co.: ca. 3.5 air mi. ESE of Trinity, 5 May 1994, *Naczi 3808 et al*; OHIO: Adams Co., ca. 3 air mi. NE of Peebles, 16 May 1994, *Naczi 3878*.

Carex latebracteata
U.S.A.: ARKANSAS: Howard Co., ca. 4 mi. NW of Athens, 21 May 1994, *Naczi 3952 & Ford*; Polk Co., ca. 8 mi. E of Vandervoort, 20 May 1994, *Naczi 3948 & Ford*; OKLAHOMA: McCurtain Co., ca. 10 road mi. N of Broken Bow, 21 May 1994, *Naczi 3953 & Ford*.

Carex saximontana
CANADA: MANITOBA: Manitoba Wildlife Management Area, W side of Prov. Rd. 346 where road crosses Souris River, 9 June 1995, *Ford 9507 & Starr*; SASKATCHEWAN: Besant Campground and Recreation Area, ca. 30 km W of Moose Jaw, 14 June 1995, *Ford 9547 & Starr*; U.S.A.: UTAH: Utah Co., Timpanogos National Monument parking area. Along Hwy.92 E of Alpine, 10 August 1993, *Naczi 3372 & Thieret*.

Carex superata
U.S.A.: ALABAMA: Butler Co., ca. 0.5 mi N of Oaky Streak, 23 May 1994, *Naczi 3990 & Ford*; Greenville, 3 mi. N of center of town along route 263, 24 May 1994, *Naczi 3993 & Ford*; MISSISSIPPI: Tishomingo Co., ca. 10 mi N of Iuka, J. P. Coleman State Park, 25 May 1994, *Naczi 4013 et al*.

Carex willdenowii
U.S.A.: ARKANSAS: Garland Co., ca. 17 air mi. N of Hot Springs, Iron Springs Recreation Area of Ouachita National Forest, 19 May 1994, *Naczi 3924 & Ford*; OHIO: Pike Co., 1.5 road mi. W of Buchanan, 16 May 1994, *Naczi 3887*; PENNSYLVANIA: Bradford Co., ca. 8 mi. SW of Towanda, along W side of Preacher Brook Road, 17 June 1994, *Naczi 4287 & Thieret*.

Appendix 4

Collection data for achenes sampled in *Carex* section *Phyllostachys*. Vouchers are deposited at KNK and WIN unless otherwise noted. Herbarium acronyms follow Holmgren et al. (1990).

Carex backii

CANADA: BRITISH COLUMBIA: McLeese Lake 22 mi. NNW of Williams Lake, 4 June 1956, *Calder 17022 et al.* (DAO); NEW BRUNSWICK: Albert Co., Pleasant Vale, 19 June 1945, *Dore 45.198 & Gorham*. (DAO); U.S.A.: WISCONSIN: La Cross Co., Washington Twp., wooded slope bordering a branch of Coon Creek in Bohemian Valley, 19 June 1959, *Hartley 1964*. (DAO).

Carex basiantha

U.S.A. ALABAMA: Butler Co., ca. 0.5 mi N of Oaky Streak, 23 May 1994, *Naczi 3991 & Ford*; ARKANSAS: Scott Co., ca. 2 mi N of Y City, 20 May 1994, *Naczi 3938 & Ford*; FLORIDA: Gadsden Co., Flat Creek Boat Landing, 1 June 1988, *Bryson 7893 & Gholson*. (MICH); LOUISIANA: West Feliciana Parish, 0.2 mi. S of jct. of Rtes. 61 snd 10, 23 May 1994, *Naczi 3987 & Ford*; OKLAHOMA: McCurtain Co., ca. 4 mi. N of Idabel, 21 May 1994, *Naczi 3954 & Ford*; SOUTH CAROLINA: Berkeley Co., Rte. 52, 1.2 mi. N of Goose Creek, 18 May 1988, *Hill 19477*. (MICH); TENNESSEE: Scott Co., ca. 10 air mi. W of Oneida at Rte. 297 crossing of Big South Fork of Cumberland River, 22 June 1993, *Naczi 3201 & Reznicek*.

Carex jamesii

CANADA: ONTARIO: Kent Co., Orford Twp., Clear Creek, 22 May 1991, *Oldham 12554*. (MICH); U.S.A.: ALABAMA: Madison Co., E of Huntsville on Monte Sano Mt., 10 May 1985, *Bryson 3874 et al.* (MICH); INDIANA: Martin Co., ca. 4 mi. SE of Loogootee, 21 May 1913, *Deam 12,858*. (MICH); IOWA: Mills Co., Wilson Timber, 29 May 1992, *Wilson 5175*. (MICH); KENTUCKY: Mason Co., ca. 2 air mi. W of Dover along S side of Rte. 8, 29 May 1994, *Naczi 4028 & Flynn*; VIRGINIA: Lunenburg Co., 0.5 mi. N of State Rte. 612, 3 June 1986, *Wieboldt 5982*. (MICH); WEST VIRGINIA: Fayette Co., New River Gorge, about 8 mi. NE of Beckley, 20 May 1985, *Wieboldt 5523*. (MICH).

Carex juniperorum

CANADA: ONTARIO: Hastings Co., Tyendinga Twp., 5.5 km NE of Shannonville, 11 June 1991, *Catling 9102*. (MICH).; U.S.A: KENTUCKY: Lewis Co., Hughes Knob, 0.75 mi. N of East Fork Church, 7 May 1991, *Reznicek 8754 et al*. (MICH); OHIO: Adams Co., Bush Creek Twp., E of Tulip Rd. 0.6 mi. S of Lynx, 6 May 1991, *Reznicek 8748 et al*. (MICH).; Adams Co., Tiffin Twp., W of State Rd. 41, 1.5 mi. N of West Union on S side Adams Lake, 6 May 1991, *Reznicek 8742 et al*. (MICH).

Carex latebracteata

U.S.A.: ARKANSAS: Howard Co., ca. 4 mi. NW of Athens, Ouachita National Forest, 21 May 1994, *Naczi 3952 & Ford*.; Polk Co., ca. 8 mi. E of Vandervoort, 20 May 1994, *Naczi 3948 & Ford*; OKLAHOMA: McCurtain Co., ca. 10 road mi. N of Broken Bow, Hochatown State Park, 21 May 1994, *Naczi 3953 & Ford*.

Carex saximontana

CANADA: BRITISH COLUMBIA: 0.5 mi. east of Nickel Plate Mine along road between Hedley and Mt. Apex, 19 July 1953, *Calder 10729 & Savile*. (DAO); U.S.A.: MINNESOTA: Chippewa Co., Lac Qui Parle State Park, 20 June 1947, *Moore 19653 & Huff*. (DAO); NORTH DAKOTA: Bismarck, in *Bouteloua gracilis*, above thicket on hillside, 23 June 1946, *Stevens s.n.* (DAO).

Carex superata

U.S.A.: ALABAMA: Monroe Co., ca. 3 mi. W of Midway, T9N, R10E, N 1/2 of sect. 30, 23 May 1993, *Naczi 3073*; ALABAMA: Butler Co., ca. 0.5 mi. N of Oaky Streak, T7N, R15E, SE 1/4 sect. 9, 24 May 1993, *Naczi 3103*; FLORIDA: Gadsden Co., ca. 5.0 air mi. S of Chattahoochee, 24 March 1990, *Orzell & Bridges 13002*. (MICH); MISSISSIPPI: Tishomingo Co., ca. 10 mi. N of Iuka, J.P. Coleman State Park, 25 May 1994, *Naczi 4013 et al.*; TENNESEE: Franklin Co., End of Jackson Co. Ala. Rte. 56, 2 May 1971, *Kral 42454b.* (MICH).

Carex willdenowii

U.S.A.: KENTUCKY: Whitley Co., ca. 8 mi. E of Williamsburg along S side of Rte. 92, 29 May 1993, *Naczi 3153*; OHIO: Gallia Co.:,Wayne National Forest, 10 mi. SW of Gallipolis, 25 May 1988, *A.A. Reznicek 8161 & S.A. Reznicek*. (MICH); NEW YORK: Genessee Co., “The Gulf,” 6 km ENE of Le Roy, 30 May 1991, *Reznicek 8777 et al*. (MICH); PENNSYLVANIA: Warren Co., Allegheny National Forest, ca. 5 mi. E of Warren, 21 June 1985, *Rettig 1344*. (MICH); VIRGINIA: Rockingham Co., George Washington National Forest, jct. of Forest Rds. 87 and 232, 15 June 1991, *Cusick 29,658*. (MICH); WEST VIRGINIA: Pocahontas Co., Back Mountain Rd., 2 mi. NE of Wanless, 30 May 1991, *Cusick 29,595*. (MICH).