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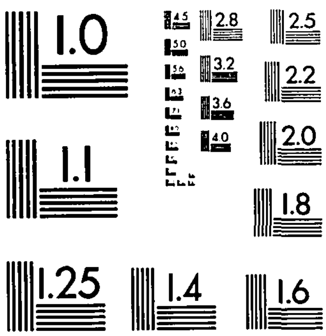

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GRADUATE COLLEGE

SYSTEMATIC STUDIES IN THE POACEAE AND CYPERACEAE

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

By

DAVID M. BRANDENBURG

Norman, Oklahoma

1985

SYSTEMATIC STUDIES IN THE POACEAE AND CYPERACEAE

A DISSERTATION

APPROVED FOR THE DEPARTMENT OF BOTANY AND MICROBIOLOGY

By

James R. Estes

Ronald J. Tyrl

John S. Fletcher

Scott L. Collins

John J. Skvarla

DISSERTATION COMMITTEE

PREFACE

This dissertation consists of five chapters, each written as a manuscript for publication. The formats of the dissertation chapters are those of the journals/books for which they have been prepared. Thus, tables and figures have been numbered independently for each chapter. The chapters and their corresponding places of publication are as follows:

Chapter 1: Bulletin of the Torrey Botanical Club

Chapter 2: American Journal of Botany

Chapter 3: Scanning Electron Microscopy

Chapter 4: <u>Vascular Flora of the Southeastern United States</u>

Chapter 5: <u>Aquatic and Wetland Plants of Kentucky</u>

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I would like to thank several individuals:

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William F. Chissoe, Charles P. Daghlian, and Scott D. Russell have been generous with both their time and expertise in aiding me in the SEM studies. Gary D. Schnell, Dan J. Hough, and Scott L. Collins assisted with the numerical analyses. Susan Heinrichs helped in the preparation of the plates in Chapter 3. Sara Fish Brown provided the line drawings for Chapter 5, and Dennis Anderson provided the drawings for Figures 6 and 7, Chapter 1.

I am appreciative of the constructive comments offered by my committee members: James R. Estes, Ronald J. Tyrl, Scott L. Collins, John J. Skvarla, and John S. Fletcher.

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CHAPTER 1

A Revision of *Diarrhena* (Poaceae) in the United States

Abstract

Two non-overlapping groups of OTU's corresponding to *Diarrhena americana* var. *americana* and var. *obovata* were revealed in cluster and principal coordinates analyses of *Diarrhena americana* (Poaceae). A stepwise discriminant functions analysis used four characters to effect complete separation of the two groups of OTU's. Two caryopsis types, differing in size, shape, beak, endosperm morphology, and degree of pericarp-seed coat fusion, occur and are correlated with the varieties. On the basis of the results obtained from the numerical analyses and morphological data, recognition of two species is warranted and the new combination *Diarrhena obovata* is made.

Diarrhena Beauv. (Poaceae) inhabits woodlands of the central and eastern United States and temperate eastern Asia (Anderson, 1958; Koyama and Kawano, 1964). Although the genus is traditionally placed in the Pooideae, its subfamilial classification is problematic (Tateoka, 1957, 1960; McFarlane and Watson, 1980; Campbell, 1985). Currently, *Diarrhena americana* Beauv. is the only recognized species in the United States, although Gleason (1952a,b) described two varieties, *D. americana* var. *americana* and *D. americana* var. *obovata* Gleason. Anderson (1958) concluded that intermediates exist between the varieties throughout their ranges, and that recognition of the taxa as species is not warranted. While preparing a treatment of *Diarrhena* for *Vascular Flora of the Southeastern United States*, I noted consistent morphological differences between the varieties; thus a reassessment of their taxonomic status seemed justified. I employed scanning electron microscopy and computer-assisted numerical techniques to evaluate the pattern of variation in *Diarrhena americana*. For brevity, *D. americana* var. *americana* will also sometimes be referred to as AMERICANA, and var. *obovata* as OBOVATA.

Materials and Methods. Nineteen morphological characters (Table 1) were measured and coded for 78 herbarium specimens (39 from each variety, _sensu_ Anderson) of _Diarrhena americana_. Characters selected were those exhibiting intertaxon variation in a preliminary analysis, as well as those used by Gleason (1952b) and Anderson (1958) to separate the varieties. Character states and their coding are given in the appendices. To insure adequate sampling, the specimens to serve as operational taxonomic units (OTU's) were chosen from across the geographic ranges of the varieties (Anderson, 1958). Thirty-seven OTU's were selected from regions of sympatry between the taxa. In addition to the 78 OTU's measured for numerical analyses, observations were made from ca. 900 herbarium specimens on loan from the following herbaria: ASPC, BHO, BKL, CINC, CLEMS, CM, DAO, DHL, DUKE, DUR, F, FARM, FLAS, FSU, GA, GH, ILL, IND, ISC, KANU, KE, KNK, KSC, KY, LL, MEM, MICH, MIN, MISS, MO, MU, MUHW, MUR, NCU, ND, NEB, NLU, NY, OKL, OKLA, OMA, OS, PAC, PENN, PH, SIU, SMS, SMU, TAES, TENN, TEX, UARK, UMO, US, USF, VDB, VPI, WIS, and WVA.

The General Similarity Coefficient of Gower was used to assess phenetic similiarity among the OTU's. I used GOWER (Hough, 1981) to produce an OTU by OTU similarity matrix based upon the 19 morphological characters. The Gower coeffecient was chosen because of its ability to handle data sets containing binary, multistate, and continuous characters (Sneath and Sokal, 1973). To determine general levels of association among OTU's, an unweighted pair-group cluster analysis (UPGMA) was generated from the similarity matrix. The cophenetic correlation coefficient was used to determine relationship between the dendrogram and the original similarity matrix.

I subjected the OTU similarity matrix to principal coordinates analysis to assess continuous variation. Because character loadings can not be derived from a Gower matrix, correlations were calculated between the original variables and the OTU scores from the first three axes of the principal coordinates analysis. Thus the relative position of each OTU along each of the first three axes could be associated with those character(s) that contributed most to the ordination. UPGMA and principal coordinates analysis were executed with the numerical-taxonomy-system-computer programs (NT-SYS; Rohlf et al., 1979).

Stepwise discriminant functions analysis was used to assess the efficacy of the cluster analysis and to identify morphological characters best discriminining between the groups defined by cluster analysis. Because the discriminant functions program (BMDP-P7M; Dixon, 1983) was incapable of handling missing data, characters with missing values were deleted from the analysis. In addition, binary characters with little or no within-group variance (e.g., callus pubescence) were deleted also. The eleven remaining characters used for the discriminant functions analysis are noted in Table 1.

I also examined features of the caryopses by scanning electron microscopy. Caryopses, selected from herbarium specimens, were mounted whole, or cross-sectioned with a razor blade, and mounted on metal stubs using double-stick tape. The specimens were coated with gold-palladium and viewed in an ETEC scanning electron microscope at an accelerating voltage of 20 kV and a working distance of 15-20 mm.

Results and Discussion. My observations and analyses of *Diarrhena americana* revealed discontinuity in the pattern of variation; two well-defined clusters appear at a phenon level of 0.7 in the phenogram generated by UPGMA (Fig. 1). Without exception, the clusters correspond to *D. americana* var. *americana* and var. *obovata*. The cophenetic correlation coefficient for the phenogram was 0.95, an indication that it was an accurate representation of the resemblance matrix.

Two spatially distinct groups corresponding to the varieties of *D. americana* also appeared in the plot of the first two axes of principal coordinates analysis (Fig. 2). Axis I and axis II accounted for 51.5% and 11% of the variance, respectively. Pubescence of the callus; shape, length, and length/width ratio of the lemma; length of the palea; pubescence of axis; and beak type of caryopsis were the characters significantly correlated with axis I ($p<0.001$). Vestiture of blades and sheaths was significantly correlated with axis II ($p<0.001$). The two clusters are separated into subclusters on axis II. In the AMERICANA group, subcluster 1 is of individuals with all sheaths pubescent, whereas subcluster 2 includes specimens with lower sheaths glabrous but upper sheaths pubescent. The OBOVATA cluster is subclustered on the basis of vestiture of sheaths and adaxial surface of blades. The numbered subclusters in Fig. 2 are characterized as follows: 1=pubescent blades and pubescent sheaths; 2=pubescent blades but upper or lower (or both) sheaths glabrous; and 3=glabrous blades and glabrous sheaths. The basis for the subclusters in OBOVATA in the phenogram is also vestiture of sheaths and blades (Fig. 1). No geographical or ecological pattern could be ascertained for any subcluster.

In a stepwise discriminant analysis, the two groups of OTU's circumscribed by the principal coordinates and cluster analyses were easily and completely separated by a combination of four characters (Fig. 3). The results of the analysis are even more significant because three characters for which there is very little or no overlap between the two varieties -- caryopsis type, callus vestiture, and axis vestiture -- were not used in the discriminant analysis. Of the characters utilized, the length of the shortest first lemma emerged as the most important in separating the OTU's into two groups. The remaining three characters in order of importance were: lemma shape, length/width ratio of second glume, and blade vestiture (Table 2). Therefore, placement of an OTU in one taxon or the other is unequivocal.

In my study of the 78 OTU's, I realized that there are two distinct caryopsis types, differing in size (Table 4), shape of the body (Fig. 4a,b), shape of the beak (Fig.

4c,d), endosperm morphology (Fig. 4e,f), and degree of pericarp-seed coat fusion (Fig. 4e,f). Caryopses of OBOVATA have a bottlenose-shaped beak with the body abruptly widened below (Fig. 4b,d). In contrast, caryopses of AMERICANA have a broad, blunt beak that tapers gently into a narrower body (Fig. 4a,c). The endosperm of AMERICANA is solid throughout (Fig. 4e), but a cross-section of OBOVATA reveals a central cavity in the otherwise solid endosperm (Fig. 4f). In addition, the pericarp of AMERICANA is fused to the seed coat in most places (Fig. 4e), whereas that of OBOVATA is mostly free from the seed coat (Fig. 4f). Examination of caryopses from plants not used as OTU's confirmed the occurrence of these two distinct types without intermediates. Beak shape in each caryopsis type, a reflection of the shape of the upper portion of the ovary, is retained throughout development (Tateoka, 1960; Schwab, 1971). The shape is apparent early in development, and the two types are readily distinguished on herbarium specimens.

Schwab (1971) studied the caryopses of *D. americana* var. *obovata* and the Asiatic *D. japonica* and *D. mandshurica*. A comparison of her descriptions and illustrations to mine indicates that the fruit body of *D. americana* var. *americana* is more similar to the fruit bodies of the Asiatic taxa than it is to those of *D. americana* var. *obovata*. Caryopses of *D. americana* var. *obovata* differ from all other species of Diarrhena in possessing a thicker, opaque pericarp covering most of the body. The pericarp is mostly thin and transparent on the other species, being thick only in places.

Diarrhena americana is confined to the United States, and the two varieties are sympatric in some areas. OBOVATA occurs predominantly in the prairie states, whereas AMERICANA occurs southeast of this region, with disjunct populations in the Ouachita and Ozark Mountains (Fig. 5). Both taxa are found in similar woodland habitats, and no phenological differences were detected from information on herbarium labels. No differences in perceived morphological patterns in areas of sympatry were observed.

Gleason (1952b) recognized two morphological varieties of Diarrhena americana. The characters he used to circumscribe the two varieties overlap (Table 3). Surprisingly, he failed to mention the presence or absence of callus hairs. Anderson (1958) reexamined the relationship between these two and found that they could be distinguished by differences in pubescence of the blades, pubescence of the inflorescences, length and width of glumes, and length, width, shape, and pubescence of lemmas. He treated D. americana, however, as a single highly variable species with two extreme morphological forms connected by intermediates. He considered Diarrhena *americana* var. *americana* to have relatively long lemmas, hairy calluses, and hirsutulous inflorescence axes; in contrast he considered *D. americana* var. *obovata* to have relatively short lemmas, glabrous calluses, and scabrous inflorescence axes. Anderson reported that intermediates occur throughout the range of *D. americana*, but he did not cite specific localities. He concluded that the only consistent difference between the forms was the presence or absence of callus hairs, a feature insufficient for him to recognize the varieties as species.

The results of my work -- numerical analyses, scanning electron microscopy, and study of over 900 herbarium specimens -- leave little doubt that these two taxa should be recognized at the species level. They are easily distinguishable at any stage of growth by a suite of correlated qualitative and quantitative morphological characters (Table 4). I suggest that previous studies of these taxa reported intermediates between them only because the characters chosen to circumscribe the two were inadequate (Table 3). I found no overlap for caryopsis type, and overlap was slight for several other characters (Table 4). No previous specific epithet exists for *D. americana* var. *obovata*; hence, I have made the appropriate new combination.

Taxonomic Treatment

DIARRHENA Beauv.

Perennials from scaly rhizomes; rhizomes 1.5-5 mm in diam. Culms slender and arching, unbranched, cespitose or rarely solitary; internodes hollow below, solid above; terete or compressed; leaves basal and low cauline. Sheaths open, rounded to ± keeled, longer than internodes; margins narrowly hyaline, entire or ciliate; auricles absent or present and formed from union of sheath margins and lateral extensions of ligules. Ligules stiff membranes, glabrous; apex rounded and ciliolate. Collars light green or yellowish, cartilaginous-thickened and somewhat flared at margins. Blades elongate, flat; midvein present, sometimes inconspicous, typically eccentric; apex long tapering; base tapering. Inflorescence a narrow panicle racemose at apex, long exserted and arching; primary branches ascending or appressed, one or two per node, longest branches at lowermost nodes, and progressing to subsessile solitary spikelets at uppermost nodes; apices of culms and branches terminating in a spikelet. Spikelets ± cylindrical when young, laterally compressed at maturity; terminal floret reduced and sterile, sometimes with additional included rudimentary floret; remaining florets fertile; pedicels scabrous; rachilla joints stout, ± flattened, disarticulation above the glumes and below the florets. Glumes chartaceous; apex acute; margins entire to ciliolate; nerves parallel; first glume 1/3 to 2/3 as long as second glume, less than 1/2 as long as first lemma, lanceolate, glabrous or scaberulous near apex of keel. Lemmas awnless, ± rounded on the back, chartaceous; nerves 3, prominent, convergent; apex with sharp cusp ca. 1-2 mm long; margins hyaline, entire to ciliolate; callus glabrous or pubescent. Paleas chartaceous, dorsally compressed between keels, elliptic in profile, clawed at base, 1/2 as long to ca. 1 mm shorter than lemma; margins narrowly hyaline, entire, scaberulous, or ciliolate. Lodicules lanceolate to elliptic, often broader on one side, ca. 1.5 mm long; apex ciliolate; margins entire to somewhat lacerate. Stamens two, anthers yellow. Caryopses with loose pericarp in places or throughout; beak prominent, persistent style bases normally present; mature fruit swollen and spreading lemma and palea.

Late spring to fall; fruit maturing from late August to October.

Synoptic Key to the North American Species of *Diarrhena*

1. Callus pubescent on all mature lemmas except first; lemmas widest below the middle and gradually

tapering into a cusp at apex, those of first floret 7-11 mm long; mature fruit 1.3-1.8 mm broad, gradually tapering into a broad, blunt beak (Fig. 6) ....*D. americana*

1. Callus glabrous on all mature lemmas; lemmas widest near or above the middle and ± abruptly contracted into cusp at apex, those of first floret 4.6-7.5 mm long; mature fruit 1.8-2.5 mm broad, abruptly contracted into a bottlenosed-shaped beak (Fig. 7) ....*D. obovata*

1. *Diarrhena americana* Beauv., Ess. Agrost. 142. pl. f.2. 1812. Based on *Festuca diandra* Michx.

Festuca diandra Michx., Fl. Bor. Americana. 1:67. 1803. (Type: P!).

Diarina festucoides Raf., Med. Repos. N.Y. 5:352. 1808. (provisional name). Based on *Festuca diandra* Michx.

Festuca americana Michx. ex Beauv., Ess. Agrost. 162. 1812. Name only.

Korycarpus arundinaceus Zea ex Lag., Gen. et Sp. Nov. 4. 1816.

Roemeria zeae Roem. and Schult., Syst. Veg. 1:61, 287. 1817.

Diarina sylvatica Raf. Journ. Phys. Chim. 89:104. 1819. Based on *Festuca diandra* Michx.

Diarrhena diandra Wood, Class-book of Botany. Ed. 2. 612. 1848. Based on *Festuca diandra* Michx.

Corycarpus diandrus Kuntze, Rev. Gen. Pl. 2:772. 1981. Based on *Festuca diandra* Michx.

Diarrhena festucoides Fernald, Rhodora. 34:204. 1932. Based on *Diarina festucoides* Raf.

Diarrhena arundinacea Rydb., Fl. Prairies and Plains Centr. N. Amer. 114. 1932. Based on *Korycarpus arundinaceus* Zea.

Culms 6.0-13.1 dm tall, glabrous or pubescent. *Sheaths* pubescent, less commonly glabrous, or pubescent only near collar; auricles pubescent. *Ligules* 0.5-1.8 mm long. *Collars* pubescent, rarely glabrous. *Blades* 25-51 cm long, 7-20 mm wide, glabrous or scaberulous above and below; margins scaberulous or somtimes ciliate. *Inflorescence* 9-30 cm long, bearing 4-23 spikelets; axis scabrous and also with few to many scattered hairs 0.5 mm or longer;

nodes 4-10; primary panicle branches to 12 cm long, bearing 2-6 spikelets. Spikelets oblong to elliptic, 10-20 mm long; florets (2)4-5(7); rachilla joints ca. 2 mm long, glabrous or scaberulous, sometimes shortly pubescent at apex. Glumes green to green-stramineous; first glume 1.7-4.2 mm long, 0.3-0.7 mm wide in profile, nerves (1)3(5); second glume 2.8-6.4 mm long, 0.6-1.2 mm wide in profile, nerves (3)5. Lemmas green to green-stramineous, lanceolate in profile, tapering to apex; 5.3-10.8 mm long, first lemma 7.1-10.8 mm long; glabrous to scaberulous; callus of first lemma glabrous, those of remaining mature florets with a tuft of hairs (may be sparse) to ca. 1 mm long, most prominent on lateral margins. Paleas glabrous or scaberulous, scabrous along upper 2/3 of keels; apex usually bifid with notch (0.1)0.2-0.7 mm deep. Anthers (1.7)2.0-2.9(3.5) mm long. Caryopses 4.6-5.8 mm long, 1.3-1.8 mm broad, narrowly lanceolate in outline, body gently widening below beak; beak blunt and broad, with shallow depression; beak stramineous, shiny, and continuous with stramineous areas below, remainder of fruit black or blackish-brown, rarely orange-brown, wrinkled or sometimes smooth. (no chromosome count reported).

1. *Diarrhena obovata* (Gleason) Brandenburg, *comb. nov.*

Diarrhena americana var. *obovata* Gleason, Phytologia 4:21. 1952. (Type: NY!).

Culms 4.8-13.1 dm tall, glabrous. *Sheaths* glabrous or pubescent; auricles glabrous or pubescent. *Ligules* 0.2-1.0 mm long. *Collars* glabrous or pubescent. *Blades* 24-72 cm long, 6-18 mm wide, lower surface glabrous or scaberulous; upper suface glabrous, scaberulous, or pubescent; margins scaberulous, rarely entire. *Inflorescence* 5-30 cm long, bearing 4-33 spikelets; axis scabrous; nodes 4-8; primary panicle branches to 10 cm long, bearing 2-5(10) spikelets. *Spikelets* oblong to oval, 7-17 mm long; florets (2)3-5(7); rachilla joints ca. 1.3 mm long, glabrous. *Glumes* green to stramineous; first glume 1.7-3.7 mm long, 0.3-0.6 mm wide in profile, nerves 1 or 3; second glume 2.2-5.2 mm long, 0.75-1.5 mm wide in profile, nerves (3)5. *Lemmas* green to stramineous, obovate or elliptic in profile, less commonly broadly lanceolate, abruptly tapering into a sharp cusp at apex; 3.7-7.6 mm long, first lemma 4.6-7.5 mm long; glabrous; callus glabrous. *Paleas* glabrous, scabrous along upper 1/2 of keel; apex shallowly notched to bifid with notch 0.5-0.3(0.5) mm deep, rarely truncate. *Anthers* 1.4-2.0 mm long. *Caryopses* 4.1-6.0 mm long, 1.8-2.5 mm broad, broadly elliptic to obovate in outline, body abruptly widening below beak; beak bottlenose-shaped, cleft at apex; mostly stramineous and shiny with occasional wrinkled or smooth dark brown or red-brown areas below. (n=30, Anderson, 1958; Schwab, 1971).

Literature Cited

ANDERSON, D. E. 1958. Taxonomy and distribution of the genus Diarrhena. Master's thesis, Iowa State University, Ames.

CAMPBELL, C. S. 1985. The subfamilies and tribes of Gramineae (Poaceae) in the Southeastern United States. J. Arnold Arbor. 66:123-199.

DIXON, W. J., (ed.). 1983. BMDP statistical software. 1983 printing with additions. University of California Press, Berkeley.

GLEASON, H. A. 1952a. Change of name for certain plants of the 'manual range'. Phytologia 4:20-25.

GLEASON, H. A. 1952b. Diarrhena, in the new Britton and Brown illustrated flora of the Northeastern United States and adjacent Canada. Vol. 1. The Pteridophyta, Gymnospermae and Monocotyledoneae. Lancaster Press, Lancaster, Pennsylvania.

HOUGH, D. 1981. GOWER. Software written for the IBM 3081, Oklahoma Biological Survey, University of Oklahoma, Norman.

KOYAMA, T. and S. KAWANO. 1964. Critical taxa of grasses with North American and Eastern Asiatic distribution. Canad. J. Bot. 42:859-884.

MACFARLANE, T. D. and L. WATSON. 1980. The circumscription of Poaceae subfamily Pooideae, with notes on some controversial genera. Taxon 29:645-666.

ROHLF, F. J., J. KISHPAUGH, and D. KIRK. 1979. Numerical taxonomic system of multivariate statistical programs. Tech. Rep. State Univ. New York, Stony Brook.

SCHWAB, C. A. 1971. Floral structure and embryology of *Diarrhena* (Gramineae). Doctoral dissertation, Iowa State University, Ames.

SNEATH, P. H. A. and R. R. SOKAL. 1973. Numerical taxonomy. W.H. Freeman and Co., San Francisco.

TATEOKA, T. 1957. Notes on some grasses. III. 5. Affinities of the genus *Brylkinia*. 6. Systematic position of the genus *Diarrhena*. Botan. Mag. (Tokyo) 70:8-12.

_______. 1960. Notes on some grasses. X. Some thoughts on Festuceae, Festucinae with special reference to their morphology. Canad. J. Bot. 38:951-967.

Table 1. Characters of _Diarrhena americana_ selected for analysis.

1. vestiture of lowermost sheath 2. vestiture of uppermost sheath *3. vestiture of adaxial surface of blades 4. vestiture of callus of lemma (except first floret) *5. shape of lemma *6. shortest first glume *7. longest first glume *8. shortest second glume *9. longest second glume *10. shortest first lemma *11. longest first lemma *12. length of first palea 13. length of caryopsis 14. width of caryopsis 15. length/width ratio of caryopsis 16. vestiture of inflorescence axis *17. length/width ratio of second glume *18. length/width ratio of lemma 19. type of beak on fruit

* denotes characters used in the discriminant functions analysis

Table 2. Statistics for stepwise discriminant functions analysis.

Character - in order of entry	F-value to Enter
1. shortest first lemma	317.97
2. shape of lemma	36.62
3. length/width ratio of second glume	11.17
4. vestiture of adaxial surface of blades	4.62

Table 3. Criteria used by Gleason (1952b) to differentiate the two varieties of *Diarrhena americana*.

Character	AMERICANA	OBOVATA
panicle axis	hirsutulous	scabrous
first glume length	2.2 - 4.0 mm	1.9 - 2.8 mm
second glume length	4.0 - 5.4 mm	2.4 - 4.3 mm
lemma shape	ovate	obovate
lemma apex	long acuminate	abruptly rounded into short cusp
lemma length	7.0 -10 mm	5.2 - 6.8 mm

Table 4. Diagnostic features of the North American species of *Diarrhena*.

	AMERICANA	OBOVATA
vestiture of lemma callus (except first floret)	pubescent	glabrous
vestiture of inflorescence axis	scabrous and with some hairs $\geq$0.5 mm	scabrous
beak of caryopsis	broad and blunt	bottlenosed
shape of lemma	lanceolate	obovate or elliptic
apex of lemma	gently tapering to cusp	abruptly tapering to cusp
length/width ratio of second glume	4.0-6.6	2.7-4.3
length/width ratio of first lemma	4.7 - 7.2	3.1-4.5
length/width ratio of mature fruit	3.0-4.1	2.0-2.8
shortest first lemma	7.1-9.5 mm	4.6-6.6 mm
width of mature fruit	1.3-1.8 mm	1.8-2.5 mm

Fig. 1. Phenogram generated using the General Similarity Coefficient of Gower and UPGMA for OTU's representing North American *Diarrhena*. The correlation coefficient is 0.95.

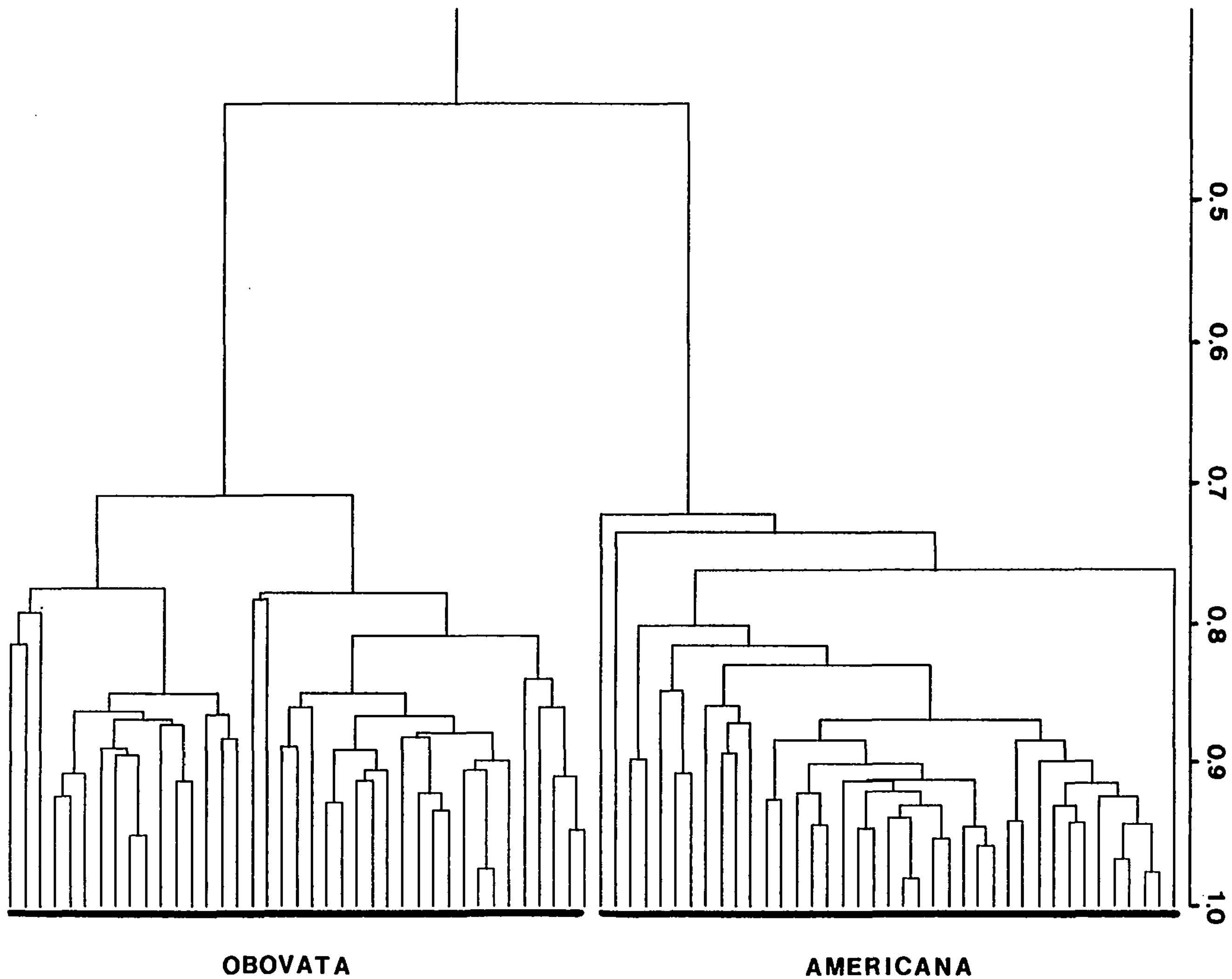

0.5
0.6
0.7
0.8
0.9
1.0
OBOVATA
AMERICANA

Fig. 2. OTU's of North American Diarrhena plotted with respect to the first two axes of principal coordinates analysis. Subclusters are as follows: AMERICANA: 1 = all sheaths pubescent; 2 = lower sheaths glabrous, upper sheaths pubescent. OBOVATA: 1 = pubescent blades and pubescent sheaths; 2 = pubescent blades but upper or lower (or both) sheaths glabrous; 3 = glabrous blades and glabrous sheaths.

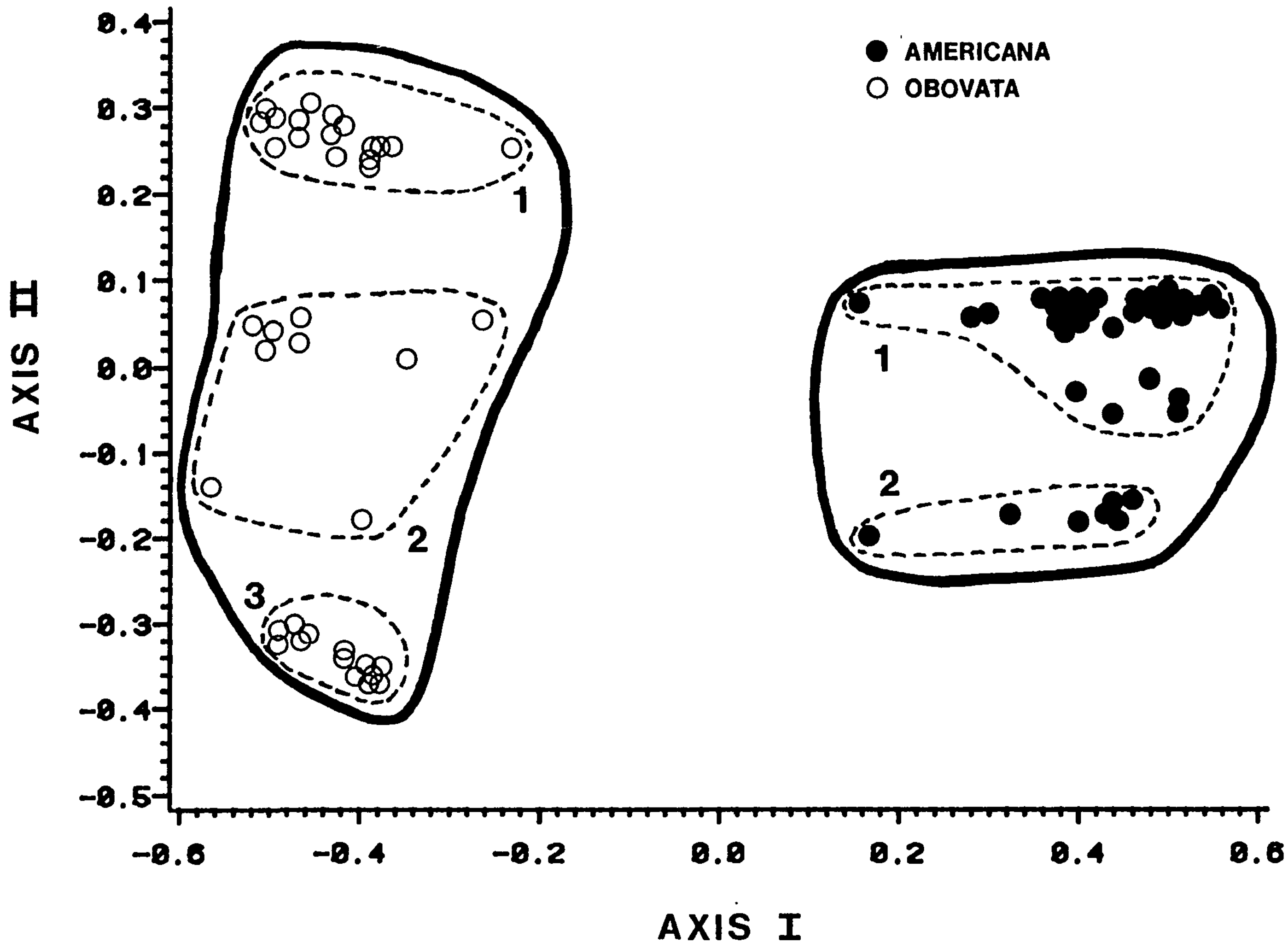
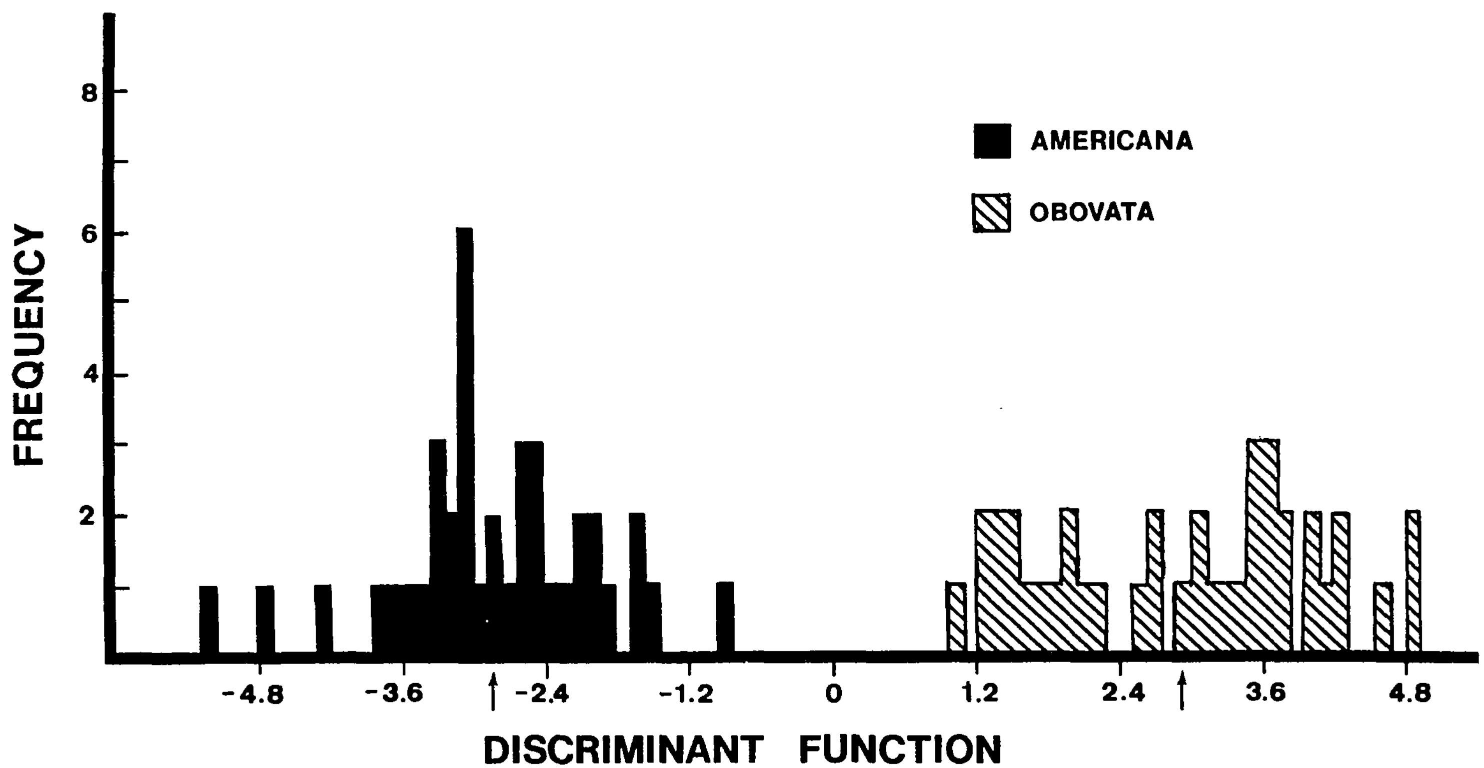

AMERICANA
OBOVATA
AXIS II
AXIS I
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
1
2
3
1
2

Fig. 3. Projection of OTU's of AMERICANA and OBOVATA onto the discriminant function axis. Arrows indicate mean values for each group.



AMERICANA
OBOVATA
FREQUENCY
8
6
4
2
-4.8
-3.6
-2.4
-1.2
0
1.2
2.4
3.6
4.8
DISCRIMINANT FUNCTION

Fig. 4. Caryopses of North American *Diarrhena*. AMERICANA (*Ahles*, *6955*: ILL): (a) whole caryopsis (x8.5); (c) beak (x45); (e) cross-section (x35), lower arrow = fusion of pericarp and seed coat, upper arrow = endosperm solid in center. OBOVATA (*Anderson*, *1072*: ISC): (b) whole caryopsis (x8.5); (d) beak (x45); (f) cross-section (x30), lower arrow = pericarp free from seed coat, upper arrow = central cavity in endosperm.

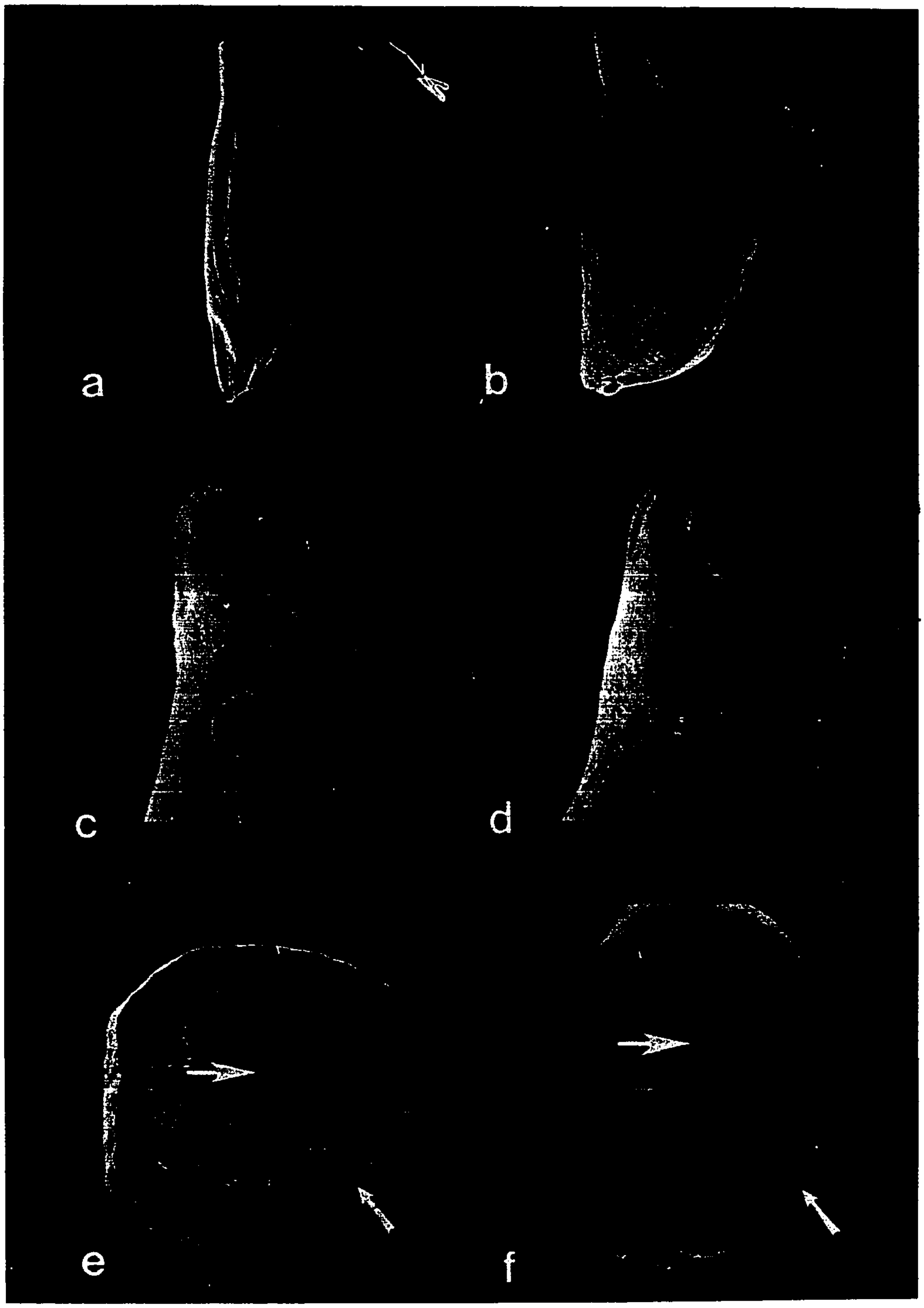

a
b
c
d
e
f

Fig. 5. Documented distribution of North American *Diarrhena*.

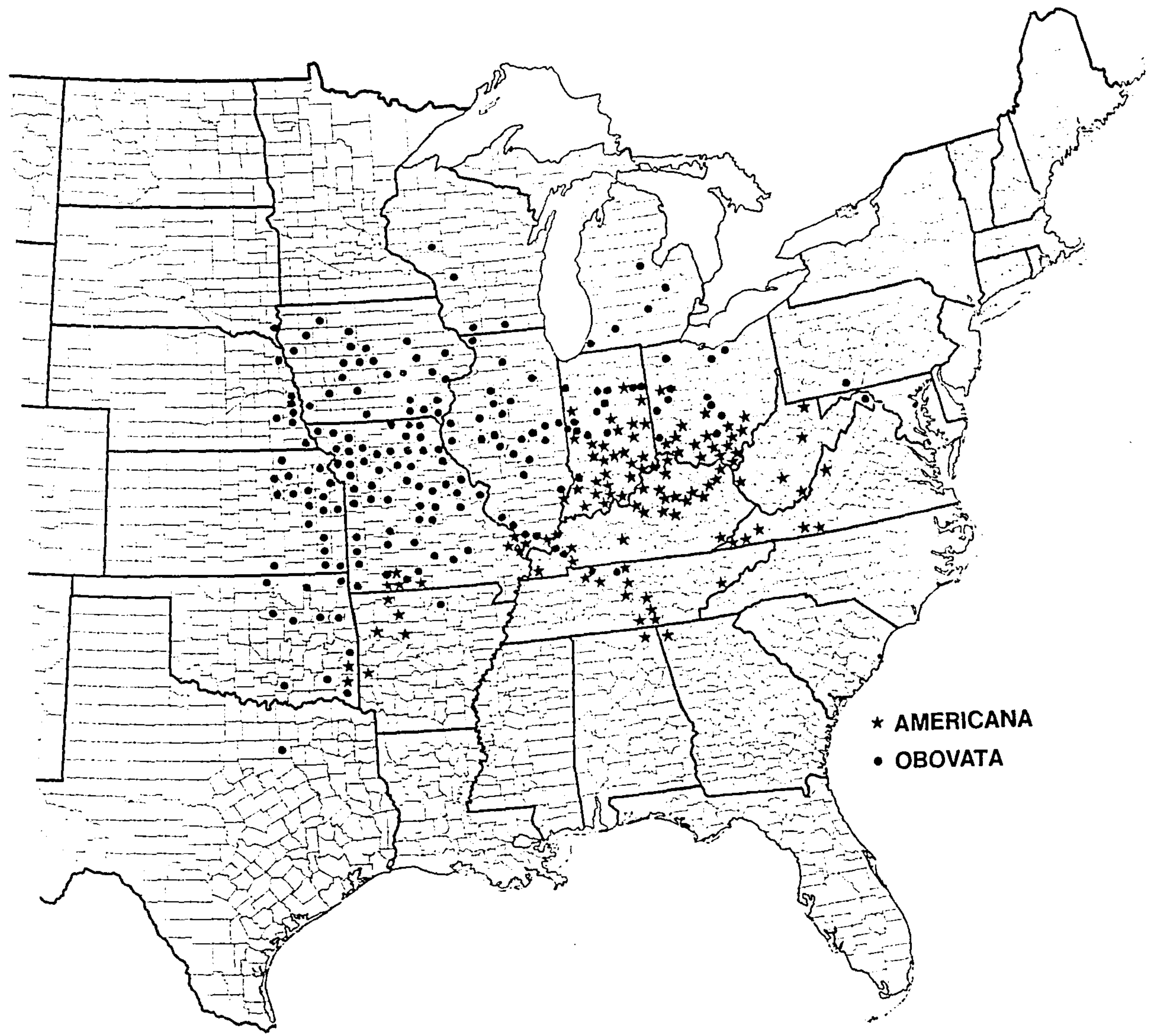

★ AMERICANA
● OBOVATA

Fig. 6. Illustrations of _Diarrhena americana_. (a) mature spikelet (x5); (b) callus of lemma (x20); (c) caryopsis (x5); (d) inflorescence axis (x20); (e) lemmas (x5); (f) immature spikelet (x5).

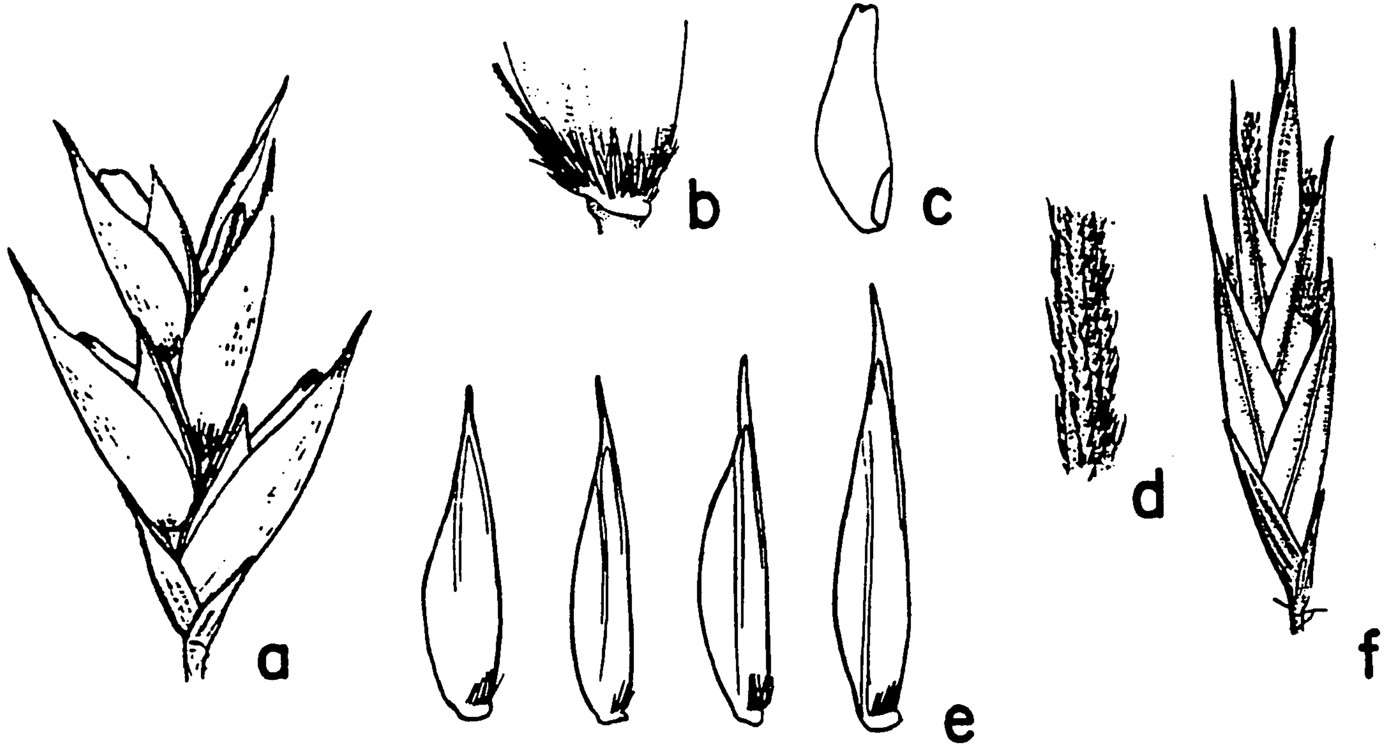
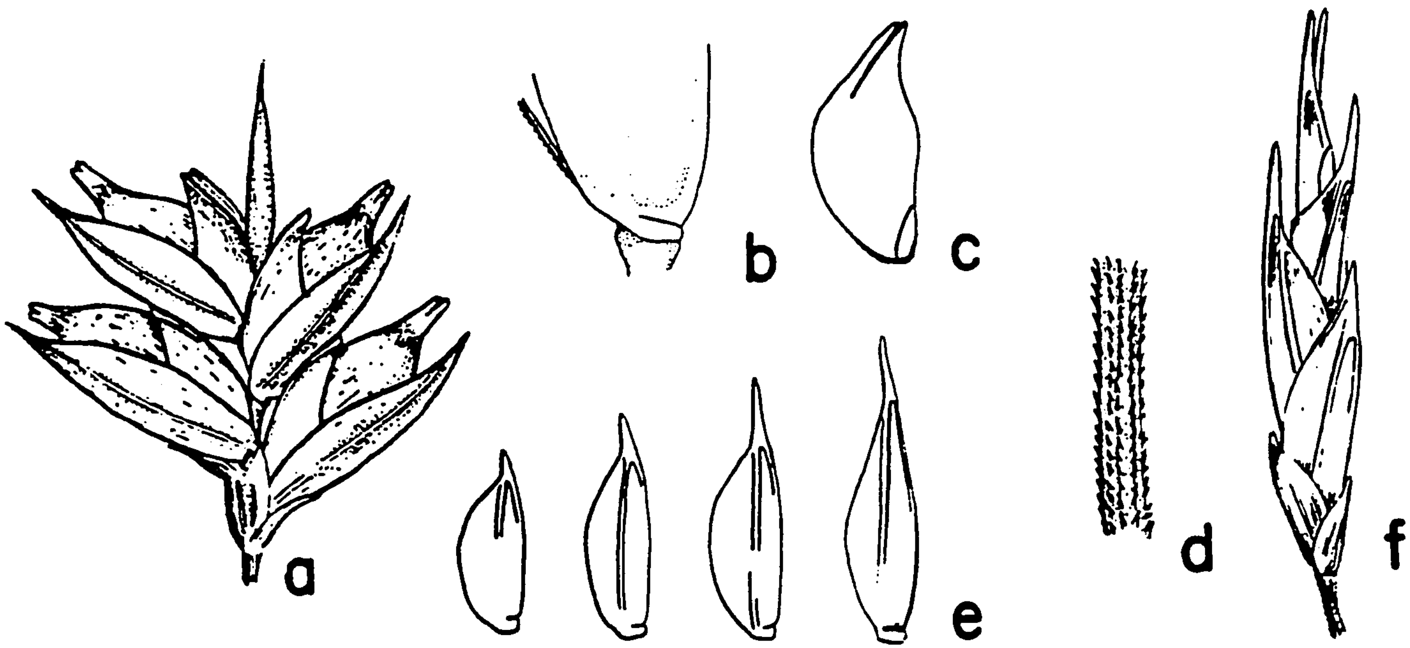

a
b
c
d
e
f

Fig. 7. Illustrations of Diarrhena obovata. (a) mature spikelet (x5); (b) callus of lemma (x20); (c) caryopsis (x5); (d) inflorescence axis (x20); (e) lemmas (x5); (f) immature spikelet (x5).


a
b
c
d
e
f

APPENDICES

Appendix A. Characters initially examined for use in numerical analyses of North American *Diarrhena*.

I. Culms

A. vestiture of internodes

B. number of leaves

C. position of leaves

II. Sheaths

A. compression

B. length relative to internodes

C. margins

D. vestiture of lowermost

E. vestiture of uppermost

III. Ligules

A. form

B. length

C. vestiture

D. apex

IV. Collars

V. Blades

A. width

B. vestiture of abaxial surface

C. vestiture of adaxial surface

D. margin

E. base

VI. Inflorescences

A. length

B. width

C. number of inflorescence branches

D. branch length

E. number of branches per node

F. vestiture of axis

VII. Spikelets

A. length

B. number of florets

C. pedicels

D. rachilla

VIII. Glumes

A. length

B. width

C. length/ width ratio

D. shape

E. nervation

F. vestiture

G. margins

H. apex

IX. Lemmas

A. length

B. width

C. length/width ratio

D. shape

E. nervation

F. vestiture

G. margins

H. apex

I. callus

X. Paleas

A. length

B. width

C. length/width ratio

D. shape

E. nervation

F. vestiture

G. margins

H. apex

XI. Stamens

A. number

B. anther length

XII. Fruits

A. length

B. width

C. length/width ratio

D. shape

E. color

F. texture

G. beak

Appendix B. Selection and coding of characters used in numerical analyses of *Diarrhena americana*.

Vestiture of lowermost sheath: 0=glabrous 1=pubescent

Vestiture of uppermost sheath: 0=glabrous 1=pubescent

Vestiture of adaxial surface of blades: 0=glabrous 1=pubescent

Vestiture of callus: 0=glabrous 1=pubescent

Vestiture of inflorescence axis: 0=no hairs ≥ 0.5mm 1=at least some hairs ≥ 0.5 mm

Shape of lemma: 0=obovate 1=elliptic 2=lanceolate

Shape of the beak of the fruit: 0=blunt and broad 1=bottlenosed

Shortest first glume: 7-10 measurements per specimen

Longest first glume: 7-10 measurements per specimen

Shortest second glume: 7-10 measurements per specimen

Longest second glume: 7-10 measurements per specimen

Shortest first lemma: 7-10 measurements per specimen

Longest first lemma: 7-10 measurements per specimen

Length of first palea: average of 3 measurements

Length of fruit: average of 3 measurements

Width of fruit: average of 3 measurements

Length/width ratio of fruit: average of 3 ratios

Length/width ratio second glume: average of 3 ratios

Length/width ratio of first lemma: average of 3 ratios

Appendix C. Basic data matrix for numerical analyses of North American *Diarrhena*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
A01	0.0	1.0	0	1.0	2	4.6	6.2	3.8	5.8	8.2	10.0	5.0	5.0	1.6	3.1	1	4.9	5.6	0
A02	1.0	-9.9	0	1.0	2	2.2	3.1	3.7	4.6	7.5	8.4	5.0	-9.9	-9.9	-9.9	1	4.0	5.5	0
A03	1.0	1.0	0	1.0	2	2.7	3.1	3.3	5.0	7.5	8.3	4.9	-9.9	-9.9	-9.9	1	4.8	5.1	0
A04	1.0	1.0	0	1.0	2	2.9	3.6	4.6	5.0	7.9	9.1	5.0	-9.9	-9.9	-9.9	0	5.2	6.1	0
A05	1.0	1.0	0	1.0	2	2.9	3.3	4.3	4.9	8.7	9.6	5.3	-9.9	-9.9	-9.9	1	5.4	6.8	0
A06	1.0	1.0	0	-9.9	2	2.3	3.9	4.4	5.6	8.7	9.7	5.2	5.3	1.6	3.3	1	4.9	6.5	0
A07	-9.9	1.0	0	1.0	2	2.2	3.3	4.3	4.7	8.3	9.5	5.2	-9.9	-9.9	-9.9	1	4.8	7.2	0
A08	1.0	1.0	0	1.0	2	3.0	3.7	4.3	5.2	8.3	9.1	5.3	5.3	1.7	3.1	1	4.6	5.8	0
A09	1.0	-9.9	0	1.0	2	2.9	4.2	4.2	5.3	8.1	10.0	4.8	4.9	1.6	3.0	1	4.6	5.7	0
A10	0.0	1.0	0	1.0	2	2.8	3.7	4.3	5.5	7.1	8.3	5.1	-9.9	-9.9	-9.9	1	4.6	6.6	0
A11	1.0	1.0	0	1.0	2	2.5	3.3	4.7	5.6	8.5	9.3	5.4	-9.9	-9.9	-9.9	1	5.0	5.7	0
A12	1.0	1.0	0	1.0	2	2.5	3.2	4.0	4.6	8.3	9.6	5.2	-9.9	-9.9	-9.9	1	4.4	6.0	0
A13	1.0	1.0	0	1.0	2	2.7	3.1	3.7	4.5	7.9	9.1	5.2	-9.9	-9.9	-9.9	1	5.3	5.8	0
A14	1.0	1.0	0	1.0	2	2.9	3.3	4.8	5.4	8.5	10.0	5.4	-9.9	-9.9	-9.9	1	5.2	7.0	0
A15	1.0	1.0	0	1.0	2	3.2	4.2	4.9	6.0	9.1	10.8	5.3	-9.9	-9.9	-9.9	1	6.3	6.6	0
A16	0.0	1.0	0	1.0	2	2.5	3.5	4.9	5.7	8.7	9.7	5.4	5.3	1.8	2.9	1	6.0	6.4	0
A17	1.0	1.0	0	1.0	2	2.0	2.9	3.8	4.6	7.3	8.3	4.9	4.9	1.6	3.0	1	4.3	5.7	0
A18	1.0	1.0	0	1.0	2	2.5	3.3	4.0	4.6	7.9	8.5	5.1	-9.9	-9.9	-9.9	1	5.4	6.4	0
A19	1.0	1.0	0	1.0	2	2.7	3.3	4.1	4.8	9.0	10.0	5.2	-9.9	-9.9	-9.9	1	4.7	5.8	0
A20	1.0	1.0	0	1.0	2	1.8	2.5	3.8	4.2	6.2	7.1	4.7	-9.9	-9.9	-9.9	1	4.5	5.0	0
A21	1.0	1.0	0	1.0	2	2.5	3.9	4.7	6.1	8.7	10.0	5.5	-9.9	-9.9	-9.9	1	4.9	5.6	-9.9
A22	0.0	1.0	0	1.0	2	2.2	2.9	3.9	4.6	7.9	8.3	5.4	-9.9	-9.9	-9.9	1	4.8	5.6	0
A23	0.0	1.0	0	1.0	2	2.6	3.6	4.2	5.0	7.6	8.9	5.3	-9.9	-9.9	-9.9	1	4.7	5.6	0
A24	1.0	1.0	0	1.0	2	2.2	3.3	3.9	4.4	7.1	8.3	5.0	-9.9	-9.9	-9.9	1	4.5	4.9	0
A25	-9.9	1.0	0	1.0	2	2.5	3.4	4.1	5.4	8.1	9.6	5.0	-9.9	-9.9	-9.9	1	5.1	5.5	0

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
A26	1.0	1.0	0	1.0	2	2.1	3.1	4.1	5.0	8.3	9.7	5.2	-9.9	-9.9	-9.9	1	5.8	6.0	0
A27	-9.9	1.0	0	1.0	2	2.1	2.7	3.7	4.6	7.9	9.6	5.3	-9.9	-9.9	-9.9	1	4.1	5.4	0
A28	1.0	1.0	0	1.0	2	2.5	3.3	3.3	4.2	7.5	8.7	5.0	-9.9	-9.9	-9.9	1	4.4	5.4	0
A29	1.0	1.0	0	1.0	2	2.8	3.7	4.5	5.7	8.1	9.3	5.3	6.1	1.7	3.7	1	5.2	5.6	0
A30	1.0	1.0	0	1.0	2	1.7	2.5	2.8	3.7	5.8	6.6	4.1	-9.9	-9.9	-9.9	1	4.0	3.9	0
A31	1.0	1.0	0	1.0	2	2.5	3.0	4.1	4.6	8.7	8.7	5.0	-9.9	-9.9	-9.9	1	5.2	6.6	0
A32	0.0	1.0	0	1.0	2	2.1	2.7	3.3	4.2	7.1	7.9	5.2	-9.9	-9.9	-9.9	0	4.7	4.7	0
A33	1.0	1.0	0	1.0	2	3.2	4.7	5.0	6.2	9.5	10.4	5.8	6.1	1.5	4.1	1	6.6	6.3	0
A34	1.0	1.0	0	-9.9	2	2.5	2.9	3.9	4.2	8.4	9.3	5.5	5.8	1.7	3.5	0	4.6	5.6	0
A35	1.0	1.0	0	1.0	2	2.6	3.5	4.6	5.4	7.9	9.6	5.4	5.3	1.4	3.9	1	5.1	6.0	0
A36	1.0	1.0	0	1.0	2	2.1	2.9	3.7	5.0	6.6	8.6	5.3	5.9	1.7	3.4	1	4.4	5.0	0
A37	1.0	1.0	0	1.0	2	2.5	3.8	4.5	6.1	8.7	10.1	5.5	5.6	1.8	3.1	1	5.3	5.7	0
A38	1.0	1.0	0	1.0	2	2.1	3.0	3.7	4.7	7.9	8.7	5.2	5.6	1.6	3.5	1	4.6	5.7	0
A39	0.0	1.0	0	1.0	2	2.9	3.3	4.8	5.4	8.3	9.1	4.9	5.5	1.6	3.5	0	5.3	5.5	0
001	0.0	1.0	1	0.0	0	1.9	2.8	2.8	3.9	5.6	6.0	4.0	-9.9	-9.9	-9.9	0	3.8	3.3	1
002	1.0	1.0	1	0.0	0	2.1	2.9	2.9	3.5	5.0	6.2	3.9	4.8	2.1	2.2	0	2.8	4.0	1
003	1.0	1.0	1	0.0	0	1.8	2.7	2.5	3.3	4.6	6.0	4.2	-9.9	-9.9	-9.9	0	3.6	3.3	1
004	1.0	1.0	1	0.0	0	2.2	3.4	3.3	3.8	5.4	7.0	3.7	4.7	2.4	1.9	0	4.3	3.6	1
005	1.0	1.0	1	0.0	0	1.8	2.9	2.5	3.3	5.0	5.4	3.7	-9.9	-9.9	-9.9	0	3.3	3.8	1
006	0.0	0.0	0	0.0	0	1.3	2.7	2.9	3.3	4.6	5.4	3.9	4.7	2.0	2.4	0	3.4	3.7	1
007	0.0	0.0	1	0.0	2	2.2	3.5	3.0	4.6	5.2	6.2	4.3	5.4	2.2	2.5	0	3.2	3.6	1
008	1.0	1.0	1	0.0	0	1.9	3.5	2.7	3.6	5.2	6.1	3.4	4.1	2.0	2.1	0	4.0	3.7	1
009	0.0	1.0	1	0.0	1	1.8	2.5	2.3	3.2	4.6	5.4	3.8	4.9	2.3	2.1	0	2.7	3.5	1
010	0.0	0.0	0	0.0	0	1.8	2.3	2.7	3.4	5.4	6.2	4.2	-9.9	-9.9	-9.9	0	3.3	3.4	1
011	0.0	0.0	0	0.0	0	2.1	3.3	2.7	4.2	6.2	7.1	4.2	-9.9	-9.9	-9.9	0	3.7	3.9	1

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
012	0.0	0.0	0	0.0	0	1.6	2.5	2.7	3.7	5.4	7.1	3.9	5.5	2.3	2.4	0	3.6	4.0	1
013	1.0	1.0	1	0.0	1	2.7	3.6	4.2	5.2	6.6	7.3	4.5	-9.9	-9.9	-9.9	0	3.9	4.2	1
014	1.0	1.0	1	0.0	1	1.9	2.3	2.8	3.3	6.2	7.1	4.4	-9.9	-9.9	-9.9	0	3.8	4.1	1
015	0.0	0.0	0	0.0	1	2.1	3.1	3.0	3.9	4.6	5.4	3.7	4.9	2.3	2.1	0	3.5	4.0	1
016	1.0	1.0	1	0.0	0	2.1	3.3	3.3	4.2	5.0	6.6	4.3	-9.9	-9.9	-9.9	0	3.8	3.5	1
017	1.0	1.0	1	0.0	0	1.7	2.2	2.7	3.1	4.7	6.0	3.8	5.1	2.3	2.2	0	2.9	4.0	1
018	1.0	0.0	1	0.0	1	1.7	2.9	2.2	3.8	5.0	6.0	4.1	5.0	2.0	2.5	0	3.7	4.4	1
019	0.0	1.0	1	0.0	1	2.7	3.4	3.3	4.4	6.0	7.1	4.8	-9.9	-9.9	-9.9	0	3.7	4.0	1
020	0.0	1.0	1	0.0	0	2.1	2.9	3.5	4.2	5.4	6.2	4.4	-9.9	-9.9	-9.9	0	3.7	3.6	1
021	0.0	0.0	0	0.0	1	1.7	3.3	3.1	3.3	6.1	7.1	4.2	-9.9	-9.9	-9.9	0	3.3	4.0	1
022	1.0	1.0	1	0.0	1	1.7	3.0	3.5	4.0	5.6	7.1	4.2	5.2	2.1	2.5	0	3.4	4.5	1
023	0.0	0.0	0	0.0	1	2.2	2.9	3.6	4.2	5.4	6.2	4.5	-9.9	-9.9	-9.9	0	3.6	3.8	1
024	1.0	1.0	1	0.0	1	2.2	3.4	3.2	3.7	6.0	7.0	4.3	-9.9	-9.9	-9.9	0	3.6	3.9	1
025	1.0	1.0	1	0.0	0	1.8	2.5	2.5	3.3	5.0	6.0	4.0	-9.9	-9.9	-9.9	0	3.6	4.2	1
026	0.0	0.0	0	0.0	0	2.2	3.5	3.3	4.1	5.0	6.2	4.0	-9.9	-9.9	-9.9	0	3.6	3.1	1
027	0.0	0.0	0	0.0	1	2.1	3.1	2.8	3.7	5.8	7.5	4.5	-9.9	-9.9	-9.9	0	2.9	3.3	1
028	0.0	0.0	0	0.0	1	1.7	3.3	3.1	4.0	5.0	5.8	3.7	-9.9	-9.9	-9.9	0	3.9	4.2	1
029	1.0	1.0	1	0.0	0	2.7	3.7	3.2	3.9	5.0	5.8	3.8	-9.9	-9.9	-9.9	0	3.3	3.5	1
030	1.0	1.0	1	0.0	0	2.2	3.3	3.2	4.2	6.0	6.6	4.0	-9.9	-9.9	-9.9	0	3.5	3.6	1
031	0.0	0.0	0	0.0	1	1.7	2.5	2.7	3.7	5.4	6.1	4.6	6.0	2.4	2.8	0	3.0	3.7	1
032	0.0	0.0	1	0.0	0	1.7	2.7	2.7	2.9	5.0	6.2	4.1	4.6	1.9	2.4	0	3.0	3.7	1
033	0.0	0.0	0	0.0	1	2.1	2.5	2.9	3.7	6.2	6.6	4.3	-9.9	-9.9	-9.9	0	3.1	4.4	1
034	1.0	1.0	1	0.0	1	2.5	2.9	3.2	3.7	5.0	5.4	4.3	5.8	2.1	2.7	0	3.0	3.8	1
035	0.0	1.0	1	-9.9	0	1.9	2.5	2.7	4.2	4.7	5.4	3.6	5.0	2.3	2.2	0	3.7	3.8	1
036	1.0	1.0	1	0.0	1	2.5	3.3	3.0	3.9	5.4	6.5	3.6	5.2	2.1	2.5	0	3.1	3.9	1
037	0.0	0.0	0	0.0	1	2.1	2.9	3.2	4.2	5.4	6.6	4.3	-9.9	-9.9	-9.9	0	2.9	3.9	1

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
038	1.0	1.0	1	0.0	1	1.8	2.7	3.0	3.6	5.2	6.2	4.1	4.3	1.8	2.4	0	3.3	3.7	1
039	1.0	1.0	1	0.0	0	2.2	3.6	3.5	4.2	5.4	6.3	4.0	-9.9	-9.9	-9.9	0	3.6	3.9	1

Appendix D. List of OTU's used in numerical analyses of North American Diarrhena: A01-A39 - AMERICANA; O01-O39 - OBOVATA.

OTU	State	County	Collection (herbarium)
A01	OH	Vinton	O'Dell, 1368 (BHO)
A02	IN	Hamilton	Potzger, 9317 (ILL)
A03	TN	Cheatham	Svenson, 10376 (US)
A04	IN	Jefferson	Young, s.n. (PH)
A05	IN	Knox	Deam, 41741 (PH)
A06	IL	Johnson	Ahles, 6955 (ILL)
A07	IL	Johnson	White, 1407 (SIU)
A08	IL	Pope	Hopkins, 613 (SIU)
A09	OH	Gallia	Herrick, s.n. (OS)
A10	OH	Butler	Werth, OX26b49 (MU)
A11	OH	Highland	Cusick, 21075 (MU)
A12	OK	LeFlore	Means, 3974 (OKLA)
A13	IN	Parke	Buser, 3125 (IND)
A14	IN	Putnam	Deam, 7422 (IND)
A15	IN	Warren	Deam, 11882 (IND)
A16	IN	Ripley	Friesner, 21116 (MO)
A17	IN	Vermillion	Hermann, 8446 (GH)
A18	IN	Orange	Deam, 17322 (IND)
A19	IL	Alexander	Ahles, 6753 (ILL)
A20	MO	Stone	Steyermark, 81971 (UMO)
A21	OH	Lawrence	Silberhorn, 2267 (KE)
A22	OK	McCurtain	Taylor, 24665 (KANU)

A23	TN	Marion	Clark & Ramseur, 1120 (NCU)
A24	AL	Jackson	Kral, 47574 (NCU)
A25	KY	Menifee	Conrad, 501 (NCU)
A26	AR	Polk	MacRoberts, 1891 (TAES)
A27	KY	Mercer	Wharton, 9205 (MEM)
A28	KY	Trigg	Athey, 3159 (MEM)
A29	IN	Orange	Tryon, 2022 (MIN)
A30	WV	Fayette	Grafton & McGraw, s.n. (WVA)
A31	WV	Upshur	Grose, s.n. (WVA)
A32	V	Carrol	Benedict, 3533 (VPI)
A33	IN	Crawford	Potzger, 7739 (ND)
A34	IN	Scott	Deam, 18892 (IND)
A35	IN	Hamilton	Friesner, 17354 (GH)
A36	IN	Crawford	Seigler, Smith, & Spencer, 11859a (ILL)
A37	OH	Athens	Cusick & Ortt, 17996 (KE)
A38	OH	Greene	Anliot, s.n. (OS)
A39	OH	Scioto	Jones, s.n. (OS)
001	OH	Shelby	Cusick, 15500 (OS)
002	IN	Miami	Deam, 46183 (IND)
003	IA	Henry	Lelong, 2239 (ISC)
004	KY	Livingston	Athey, 2636 (SIU)
005	OH	Franklin	Werner, s.n. (OS)
006	IL	Johnson	White, 1898 (SIU)
007	OH	Auglaize	Wetzstein s.n. (MU)
008	OH	Darke	Cusick, 15575 (MU)
009	OH	Huron	Jones, 67-9-25-1163 (MU)

010	OK	McCurtain	Tyrl, Lofgren, Brunken, & Perino, 53 (OKL)
011	OK	Washington	McDonald, 974 (OKLA)
012	OK	Cherokee	Wallis, 5364 (OKLA)
013	OH	Ross	Bartley & Pontius, 621 (NY)
014	IA	Greene	Monson, 588 (ISC)
015	IN	Knox	Deam, 24165 (IND)
016	IN	Clinton	Deam, 50656 (IND)
017	IL	Vermilion	Jones, 13245 (ILL)
018	IN	Putnam	Grimes, 769 (ILL)
019	IL	Tazewell	McDonald, s.n. (ILL)
020	IL	Shelby	Shildneck, C-12232 (ILL)
021	MO	Randolph	Conrad, Dimit, & Walker, 8558 (UMO)
022	MO	Jackson	Bush, s.n. (UMO)
023	MO	Linn	Crookshanks, 265 (UMO)
024	IL	Peoria	Chase, 8386 (MICH)
025	MI	Berrien	Billington, s.n. (MICH)
026	IA	Cass	Fay, 5148 (KANU)
027	KS	Cherokee	McGregor, 33425 (KANU)
028	WV	Jefferson	Core, s.n. (WVA)
029	TN	Sumner	Rogers & Rogers, 40828 (TENN)
030	TN	Wilson	Rogers & Rogers, 40882 (FLAS)
031	KS	Shawnee	Volle, 824 (KANU)
032	NE	Otoe	Stephens, 17588 (KANU)
033	OK	Cherokee	Waterfall, 9633 (TEX)
034	MO	Howard	Steyermark, 26295 (MO)

035	PA	Bedford	_Berkheimer_, _20673_ (PH)
036	IN	Vermillion	_Deam_, _37923_ (PH)
037	KS	Riley	_Norton_, _936_ (GH)
038	KS	Leavenworth	_Wagenknecht_, _3369_ (GH)
039	IL	Cass	_Geyer_, _s_._n_. (MO)

Appendix E. Representative specimens of Diarrhena obovata.

ARKANSAS: Izard Co.: bluffs of White River, 5 Aug. 1969, Thomas 16281 (SMU, ISC, NEB, NLU, VDB).

ILLINOIS: Adams Co.: Quincy, Sep. 1880, Seymour 3459 (MU); Cass Co.: Beardstown, Sep. 1842, Geyer s.n. (MO, GH, NY, PH); Champaign Co.: near Urbana, 3 Oct. 1940, Jones 13292 (ILL); Christian Co.: Taylorsville, 5 Aug. 1898, Andrews s.n. (ILL); Douglas Co.: 2 mi SE of Hugo, 12 Jul. 1971, Phillippe 560 (SIU); Fayette Co.: 1/4 mi W of rt 128, 28 Jul. 1980, Shildneck C-12254 (Fulton Co.: Canton, Wolf s.n. (ILL); Grundy Co.: Waupecan Creek Scout Camp, 2 Nov. 1964, Swink 31-c (SIU); Hancock Co.: Augusta, Jul. 1843, Mean s.n. (SIU); Jackson Co.: Cedar Lake Reservoir, 21 Sep. 1976, Heineke 1820 (SIU); Jo Daviess Co.: Apple River Canyon St. Park, 1 Sep. 1981, Heim 469 (USI) Johnson Co.: 3 mi S Vienna, 5 Sep. 1969, White 1898 (SIU); Lee Co.: Amboy, 19 Sep. 1957, Long 638 (ILL); Macon Co.: 29 Jul. 1972, Shildneck C-4310 (ILL, SIU); Menard Co.: Athens, Aug. 1860, Hall s.n. (F, NY, SIU); Peoria Co.: Pleasant Valley, 16 Aug. 1946, Chase 8386 (GA, MICH, ILL NY); Piatt Co.: Allerton Park, near Monticello, 8 Nov. 1959, Jones 28885 (ILL); Randolph Co.: along Little Mary's Creek, 31 Aug. 1973, Wilson 1750 (SIU); Sangamon Co.: NW of Springfield, 11 Oct. 1980, Shildneck C-12750 (ILL); Shelby Co.: SE of Cowden, 24 Jul. 1980, Shildneck C-12232

(ILL); Stark Co.: 4 mi NW of Wady Petra, 22 Jul. 1898, Chase 131 (MU, WIS, CLEMS, MICH, ILL, GH, ISC, MIN); Tazewell Co.: 5 mi N of East Peoria, 1 Aug. 1952, Chase 12861 (MICH, DAO); Union Co.: LaRue-Pine Hills Ecological Area, Shawnee National Forest, 28 Oct. 1979, Wilhelm and Ladd 4470 (SMS); Vermilion Co.: Fairmount, 13 Oct. 1940, Jones 13245 (ILL); Wabash Co.: Mt. Carmel, 15 Jul. 1904, Schneck s.n. (ILL); Woodford Co.: South of Spring Bay, 5 Aug. 1950, Chase 11387 (ILL).

INDIANA: Adams Co.: 2 mi NW of Decatur, 8 Sep. 1908, Deam s.n. (IND, BKL); Cass Co.: 1 mi S of Hoovers, 21 Jul. 1956, Anderson 1060 (ISC); Clinton Co.: 2 mi NE of Frankfort, 20 Jul. 1931, Deam 50656 (IND); Fountain Co.: 6 mi E of Kingman, 12 Oct. 1952, Busher 1746 (ILL, IND); Howard Co.: 4 mi W of Kokomo, 22 Aug. 1935, Elk s.n. (IND); Knox Co.: 15 mi SW of Decker, 5 Oct. 1917, Deam 24165 (IND); Marion Co.: Indianapolis, 23 Aug. 1890, Britton s.n. (PH); Miami Co.: 1 mi S of Hoover, 11 Sep. 1928, Deam 46183 (IND); Newton Co.: 28 Sep. 1932, McKee 1566 (DAO); Parke Co.: Turkey Run State Park, 12 Aug. 1937, Duncan 217 (DUKE); Putnam Co.: 3 1/2 mi S of Russellville, 3 Sep. 1911, Grimes 769 (ILL); Vermillion Co.: 3 mi W of Newport, 12 Sep. 1922, Deam 37923 (DH); Wells Co.: 11 Sep. 1898, Deam s.n. (F, MICH, MIN).

IOWA: Benton Co.: Vinto, Davis s.n. (WIS); Black Hawk Co.: Cedar Heights, 27 Jul. 1929, Burk 629 (ILL); Boone Co.: 10 mi N of Boone, 22 Aug. 1934, Fults 2788 (US, MU); Cass Co.: Cold Springs State Park, 27 Aug, 1952, Fay 5148 (KANU); Cherokee Co.: 6 mi S of Cherokee, 5 Sep. 1937, Hayden 7063 (US, ISC); Clay Co.: Peterson, 9 Sep. 1941, Hayden 8150 (ISC); Davis Co.: 7 mi E of Floris, 9 Sep. 1940, Hayden 8152; Decatur Co.: 1 Aug. 1897, Fitzpatrick 25 (US, ISC); Greene Co.: 6 mi SE of Jefferson, 8 Aug, 1955, Monson 588 (ISC); Guthrie Co.: Bear Grove Twp., 30 Aug. 1951, Fay 2121 (KANU); Hamilton Co.: Jewell Junction, 4 Jul. 1895, Cowan(?) (ISC); Henry Co.: Geode State Park, 25 Jul. 1962, Lelong 2239 (ISC); Humboldt Co.: Dakota City, Aug. 1896, Pammel s.n. (ISC); Jasper Co.: Victon Grange, 12 Jul. 1956, Van Bruggen 601 (NY); Johnson Co.: 24 Aug. 1900, Fitzpatrick & Fitzpatrick (IND); Jones Co.: Eagle Park, 7 Aug. 1956, Cooperrider 2502 (KE); Lee Co.: Sec. 14, T66N-R6W, 16 Jul. 1931, Fults 1442 (ISC); Madison Co.: Winterset, Sep. 1895, Carver 265 (MO,GH, NY, US, ISC); Mills Co.: Glenwood, 19 Jul. 1919, Pammel s.n. (ISC); Muscatine Co.: Wildcat Cave, Jul. 1906, Somes 1425 (ISC); Poweshiek Co.: Grinnell, 7 Aug 1879, Jones s.n. (US); Story Co.: Ames, 29 Jun. 1896, Ball 137 (MO, MIN, NICH, GH, NY, US, ISC); Van Buren Co.: 5 mi S Keosaugua, 27 Oct. 1939, Hayden 9243 (NY, ISC); Wapello Co.: 2 mi W Eldon, 8 Sep. 1940, Hayden 8149 (OS, ISC); Webster Co.:

Fort Dodge, 7 Jul. 1905, Somes 113 (ILL); Woodbury Co.: Sioux City, 21 Aug. 1887, (ISC).

KANSAS: Allen Co.: 2 mi S Lattarpe, 29 Sep. 1970, Stephens 45866 (KANU); Atchison Co.: Aug. 1866, Scarborough s.n. (BKL); Cherokee Co.: 1 mi W of Treece, 22 Jul. 1982, McGregor 33425 (KANU); Coffey Co.: 2 mi W, 2 mi N of LeRey, 29 Sep. 1976, Brooks 12718 (KANU); Cowley Co.: 23 mi E, 3 mi S of Winfield, 8 Oct. 1966, Koch 2500 (OKLA); Douglas Co.: 2 mi N Baldwin, 9 Sep. 1940, McGregor 337 (KANU); Franklin Co.: 5 mi W, 1 1/2 S Princeton, 10 Oct. 1973, Stephens 74401 (KANU); Geary Co.: NE corner of Jefferson Twp., 3 Oct. 1935, Gates 18676 (GH, MO); Labette Co.: 1 mi N, 3 mi W Chetopa, 30 Aug. 1977, McIntoch 79 (KANU); Leavenworth Co.: Ft. Leavenworth Mil. Reserv., 23 Sep. 1956, Wagenknecht 3369 (GH, KANU); Marshall Co.: 1/2 mi E of Erving, Lathrop 3154 (KANU); Miami Co.: 2 1/2 mi E Fontana, 25 Aug. 1970, Stephens 44227 (KANU); Neosho Co.: 7 mi E, 2 mi N Earlton, 25 Aug. 1968, Holland 2541 (KANU); Osage Co.: 1/2 mi N of Melvern, 15 Oct. 1972, Stephens 63581 (KANU); Pottawatomie Co.: 3 mi N, 3 mi W of Olsburg, 7 Aug. 1967, Barker 4340 (KANU); Riley Co.: Manhattan, 5 Sep. 1892, Carleton (NY, MO); Shawnee Co.: Lake Shawnee, 29 Aug. 1949, Volle 824 (KANU); Wabaunsee Co.: 6 mi SW of Volland, 7 Aug. 1964, Gibson 886 (OKLA).

KENTUCKY: Livingston Co.: Joy, 2 mi on Ky 133 W Ky 135, 3 Oct. 1973, Athey 2636 (SIU, MEM, VDB); Lyon Co.: Land Between the Lakes, 5 Sep. 1984, Chester 84-450 (APSC).

MICHIGAN: Berrien Co.: Warren Woods, 28 Jul. 1932, Hebert 824 (ND); Genesee Co.: Flint, Oct. 1874, Clarke 3459 (KANU, OS); Ingham Co.: East Lansing, 26 Sep. 1974, Crow 2115 (MICH); Kalamazoo Co.: E of Galesburg along Kalamazoo River, 9 Sep. 1939, Hanes 669 (MY, MIN, WIS); Midland Co.: 5 mi above Gordonville, Aug. 1938, Dreisbach 8837 (MICH).

MISSOURI: Adair Co.: Thousand Hills State Park, 15 Aug. 1954, Steyermark 76481 (UMO, US, DAO); Andrew Co.: 4 mi N of Rochester, 19 Aug. 1950, Steyermark 70019 (F); Atchison Co.: 0.8 mi W, 0.5 mi S of Dotham Store, 22 Jun. 1956, Anderson 1049 (ISC); Barton Co.: 2 mi NE of Newport, 6 Jul. 1957, Palmer 65922 (UMO, US); Boone Co.: 9 mi NE of Columbia, 17 Sep. 1969, Harmon 1652 (UMO); Buchanan Co.: 10 mi S of St. Joseph, 23 Jun. 1956, Anderson 1052 (ISC); Caldwell Co.: Wallace State Park, 27 Apr. 1969, Schwab 584 (ISC); Callaway Co.: 3 3/4 mi NW of Holts Summit, 18 Aug. 1954, Steyermark 76651 (ILL); Carroll Co.: 3/4 - 1 mi N of Mandeville, 29 Sep. 1951, Steyermark 73017 (F); Cass Co.: 4 mi SE of Pleasant Hill, 9 Oct. 1948, Steyermark 66714 (F); Chariton Co.: 5 mi W of Shannondale, 15 Sep. 1937, Steyermark 26347 (F, MO); Clay Co.: 9 Aug. 1933, Bush

12859 (PH, TEX, WIS); Clinton Co.: 6 mi S of Cameron, 27 Aug. 1934, Steyermark 14908 (MO); Cole Co.: 1 1/2 - 2 mi E of Henley, 7 May 1951, Steyermark 71174 (F); Daviess Co.: 10 mi SE of Gallatin, 10 Aug. 1952, Steyermark 74184 (F); DeKalb Co.: 1 1/2 mi SE of Weatherby, 27 Sep. 1951, Steyermark 72849 (F); Douglas Co.: 3 mi NE of Topaz, 14 Aug. 1969, Redfearn 26385 (SMS); Franklin Co.: Gray Summit, 29 Aug. 1937, Anderson (MO); Gentry Co.: 3 mi NW of Albany, 29 Aug. 1934, Steyermark 15013 (UMO,MO); Hickory Co.: along Little Niangua River, E of Jordon, 10 Jul. 1934, Steyermark 13222 (UMO, GH, US, MO); Howard Co.: 3 mi NE of Burton, 14 Sep. 1937, Steyermark 26295 (F, MO); Jackson Co.: 3 mi W of Sibley, 19 Jul. 1896, MacKenzie s.n. (F, NY, ISC, PENN, MO, MIN, KSC); Jasper Co.: Carthage, 21 Jul. 1912, Palmer 3803 (GH, NY, US, MO); Johnson Co.: Knobnoster State Park, 23 Jun. 1956, Anderson 1057 (ISC); Knox Co.: 5 mi NW of Hurdland, 19 Sep. 1950, Steyermark 70693 (F); Laclede Co.: 5 mi SW of Eldridge, 24 Jun. 1939, Steyermark 27189 (F); Lafayette Co.: 27 Jul. 1897, Demetrio 79 (GH); Lincoln Co.: 2 mi N of Whiteside, 7 Sep. 1937, Steyermark 25948 (F, MO); Linn Co.: 6-7 mi S of New Boston, 20 Sep. 1955, Steyermark 79749 (F, UMO); Livingston Co.: NW of Chillicothe, 23 Aug. 1951, Sparling 1348 (F, ISC); McDonald Co.: 24 Jul. 1893, Bush s.n. (MO); Macon Co.: 1 3/4 - 2 mi NE of Ardmore, 15 Sep. 1954, Steyermark 77367 (F, UMO); Maries Co.: Bank of Gasconade

River, Jun. 1956, *Dwyer s.n.* (F); Marion Co.: 3 mi SE of Maywood, 21 Sep. 1956, *Steyermark 82712* (F, UMO); Miller Co.: W of Capps, 20 Sep. 1938, *Steyermark 6825* (F, MO); Montgomery Co.: 1 mi S of Danville, 16 Sep. 1954, *Steyermark 77489* (F, UMO); Nodaway Co.: 4 - 4 1/2 mi NW of Barnard, 25 Sep. 1955, *Steyermark 79995* (F, UMO); Osage Co.: 3 mi NE of Gascondy, 22 Sep. 1950, *Steyermark 70868* (F, US); Pettis Co.: near Longwood, 25 Jun. 1941, *Palmer 45317* (KANU, DAO); Polk Co.: 5 mi NW of Pleasant Hope, 1 Aug. 1937, *Steyermark 24105* (F, MO); Putnam Co.: SW of Livonia, 13 Sep. 1954, *Steyermark 77218* (F, UMO); Ralls Co.: 5 mi NW of New London, 13 Aug. 1955, *Steyermark 79171* (UMO, ILL, US); Randolph Co.: along Dark Creek, 13 Aug. 1979, *Conrad, Dimit, & Walker 8558* (UMO); Reynolds Co.: Johnson's Shut-Ins State Park, 8 Aug. 1975, *Nelson 982* (SMS); Saint Louis Co.: Allenton, 30 Jul. 1893, *Letterman s.n.* (NY, US, PH, MO); Schuyler Co.: SW of Glenwood, 26 Aug. 1950, *Steyermark 70324* (F); Scotland Co.: 3 3/4 - 4 mi NE of Azen, 11 Sep. 1954, *Steyermark 77136* (KSC); Shannon Co.: 6 mi NW of Birch Tree, 2 Aug. 1969, *Redfearn, Pyrah, & Witherspoon 932* (MO, NCU, SMS); Shelby Co.: 5 mi NW of Emden, 25 Sep. 1948, *Steyermark 66603* (F); Stone Co.: near Baxter, 26 Sep. 1953, *Moore & Iltis 550* (F, WIS); Taney Co.: 6-7 mi SE of Cedar Creek, 30 Sep. 1949, *Steyermark 69475* (F); Texas Co.: Dog Bluff on Piney River, 28 Aug. 1975, *Castaner 4330* (MO); Vernon Co.: 4-5 mi W of

Virgil, 28 Sep. 1938, Steyermark 9671 (MO); Warren Co.: S of Jonesburg, 30 Sep. 1951, Steyermark 73033 (F).

NEBRASKA: Cass Co.: Weeping Water, 8 Aug. 1910, Bates 5246 (NEB, MIN); Douglas Co.: W of Florence, 17 Sep. 1897, Cleburne s.n. (NEB); Lancaster Co.: Lincoln, Jul. 1896, Thornber s.n. (MO); Otoe Co.: 5 mi S, 1 1/2 mi E of Syracuse, 6 Sep. 1962, Stephens 17588 (KANU, NY, OKLA); Richardson Co.: NE corner of Section 3, 13 Jul. 1974, Shildneck C-6831 (KANU, NEB); Sarpy Co.: Fontenelle Forest, 8 Jul. 1974, Kurtz 18 (OMA); Thurston Co.: 1 1/2 mi E jct 73 and 94, 28 Sep. 1975, Churchill 6707 (KANU, MO, NEB).

OHIO: Auglaize Co.: St. Marys, 3 Aug. 1897, Wetzstein 840 (MU); Butler Co: Middletown and Hamilton, 1834, Riddell s.n. (PH); Darke Co.: Schroder Rd., 1/2 mi S, Beamsville Rd., 23 Aug. 1976, Cusick 15575 (MU); Delaware Co.: Liberty Twp., 23 Oct. 1955, Weishaupt s.n. (OS); Fairfield Co.: Lancaster, Horr s.n. (ISC); Franklin Co.: W side of Olentangy River, 7 Nov. 1959, Cusick s.n. (OS); Henry Co.: between Napoleon and Grand Rapids, 27 Sep. 1919, Moseley s.n. (MO); Huron Co.: 1 mi N of Wakeman, 25 Sep. 1967, Jones 67-9-25-1163 (MU, KE, BHO); Lorain Co.: Sheffield, 12 Aug. 1889, Day s.n. (OS); Ross Co.: Daxto Twp., 14 Aug. 1937, Bartley & Pontius 621 (NY); Shelby Co.: Houston Cemetery, 23 Aug. 1976, Cusick 15500 (OS).

OKLAHOMA: Cherokee Co.: 2 mi N of Gibson, 7 Sep. 1957, _Wallis 5364_ (OKLA); Creek Co.: Sapulpa, 22 Jul. 1894, _Bush 827_ (MO); Johnston Co.: 0.5 mi N and 0.5 mi E of Connerville, 25 Jul. 1977, _Taylor & Wright 24977_ (DUR); Kay Co.: Tonkawa, 4 Aug. 1913, _Stevens 1861_ (OKLA, MIN, ILL, GH, NY US, MO, OKL); Leflore Co.: 3 mi SW of Bokoshe, 6 Sep. 1963, _Ball 393_ (OKLA); McCurtain Co.: 7.5 mi SW of Bethel, 7 Jul. 1972, _Taylor 11038_ (DUR); Ottawa Co.: 1/2 mi W of Wyandotte, 17 Jul. 1955, _Wallis 2503_ (OKLA); Payne Co.: Stillwater, 29 Oct. 1925, _Reatherly 171_ (ISC, OKL); Pushmataha Co.: Little River, 5 Jul. 1930, _Little & Olmsted 539_ (US, OKL); Wagoner Co.: Wagoner, 21 Aug. 1895, _Blankenship_ (GH, MO, MU); Washington Co.: SE of Bartlesville, 22 Jun. 1972, _McDonald 532_ (OKLA).

PENNSYLVANIA: Bedford Co.: 1/2 mi W of Wolfsburg, 15 Sep. 1961, _Berkheimer 20673_ (PAC, PH).

SOUTH DAKOTA: Union Co.: Elk Point, 18 Aug. 1891, _Wallace_ (US).

TENNESSEE: Montgomery Co.: 3 mi S by E of Clarsksville, 1 Aug. 1948, _Clebsch s.n._ (APSC); Sumner Co.: Lone Branch recreation area, 9 Jul. 1961, _Rogers 40828_ (TENN, MICH, FSU, SMU, VDB).

TEXAS: Dallas Co.: Dallas, Aug. 1879, _Reverchon 1116_ (GH).

WEST VIRGINIA: Jefferson Co.: Opequon Creek, 19 Aug. 1931, Core 3805 (WVA).

WISCONSIN: Eau Claire Co.: Putnam Park, 1978, Fay (WIS); Lafayette Co.: Fayette, 23 Jul. 1894, Cheney (WIS); Monroe Co.: along the Kickapoo River, 13 Aug. 1959, Melchert (WIS); Rock Co.: along Sugar River, Jun. 1961, Iltis s.n. (TEX, WIS).

Appendix F. Representative specimens of Diarrhena americana.

ALABAMA: Jackson Co.: 9.2 mi S Huntland, 11 Jul. 1972, Kral 47574 (NCU, CLEMS, VDB).

ARKANSAS: Carroll Co.: Beaver, 26 Sep. 1913, Palmer 4494 (US, MO); Franklin Co.: Salt Fork Creek, 16 Aug. 1978, Barber 1343 (UARK); Newton Co.: 2 mi NE of Boxley, 25 Oct. 1953, Iltis 4461 (UARK); Polk Co.: Old Pioneer Cemetary, 21 Jul. 1976, MacRoberts 1891 (TAES); Pope Co.: Aug. 1977, Graney (UARK).

GEORGIA: Walker Co.: Pigeon Mountain Wildlife Management Area, 28 Jun. 1982, Coile, Hill, & Coile 2944 (GA).

ILLINOIS: Alexander Co.: 2 mi W of Tamms, 29 Aug. 1952, Ahles 6753 (ILL); Hardin Co.: Blind Hollow, 30 Jul. 1951, Bailey & Swayne 1687 (SIU); Jackson Co.: Cedar Lake Reservoir, 21 Sep. 1976, Heineke 1832 (SIU); Johnson Co.: 3 mi S of Vienna, 13 Jul. 1969, White 1407 (SIU); Pope Co.: Lusk Creek, 4 Sep. 1966, Hopkins 613 (SIU); Union Co.: Atwood Ridge, 17 Oct. 1973, Wilson 2309 (SIU); Wabash Co.: Mt. Carmel, 1874, Schneck (GH).

INDIANA: Bartholomew Co.: Goshen (now Hope), 26 Jul. 1977, Schweinitz (PH); Brown Co.: 2 mi SE of Belmont, 18 Jul. 1926, Deam 43461 (IND, MIN); Crawford Co.: 3 mi N of

Sulphur, 10 Aug. 1932, Deam 52633 (IND); Dubois Co.: 3/4 mi N of Birdseye, 6 Jul. 1912, Deam 11635 (IND); Hamilton Co.: 4 mi S of Noblesville, 26 Sep. 1934, McCoy 2115 (UMO); Harrison Co.: 4 mi NE of Elizabeth, 28 Jun. 1916, Deam 20543 (IND); Hendricks Co.: 3 mi NW of Planfield, 13 Jun. 1942, Potzger 9182 (ND); Henry Co.: 2 mi W of Newcastle, 21 Jul. 1937, Kriebel 4435 (DUKE); Huntington Co.: 4 mi W of Liberty Center, 15 Aug. 1924, Deam 40957 (IND); Jay Co.: 3 1/2 mi NE of Pennville, 2 Aug. 1927, Deam 45122 (IND); Jefferson Co.: Clifty Falls State Park, 26 Jul. 1956, Anderson 1068 (ISC); Jennings Co.: ca. 1 mi N of Vernon, 9 Jul. 1911, Deam 9111 (IND); Knox Co.: ca. 5 mi NE of Mt. Carmel, ILL., 26 Jul. 1925, Deam 41741 (PH); Lawrence Co.: 2 mi W of Williams, 11 Aug. 1918, Deam 26179 (IND); Marion Co.: Shades of Death, 25 Aug. 1890, Johnson s.n. (BKL); Martin Co.: 3 mi NE of Trinity Springs, 16 Jul. 1919, Deam 28186 (IND); Munroe: W of Bloomington, 28 Jul. 1924, Blaydes 5268 (IND); Orange Co.: 1 mi N of West Baden, 14 Jul. 1915, Deam 17322 (IND); Owen Co.: 7 mi N of Spencer, 18 Jul. 1915, Deam 17556 (IND); Parke Co.: Turkey Run State Park, 6 Jul. 1967, Riggins 218 (ISC, APSC); Perry Co.: ca. 6 mi W of Derby, 4 Jul. 1912, Deam 11526 (IND); Putnam Co.: 4 mi SE of Russellville, 28 Aug. 1910, Deam 7422 (IND); Ripley Co.: 1/2 mi N of Versailles, 5 Jul. 1946, Potzger 10402 (NDO); Rush Co.: 2 mi W of Gowdy, 7 Jul. 1925, Deam 41420 (IND); Scott Co.: 2 1/2 mi N of

Lexington, 12 Jul. 1919, Deam 28017 (GH); Switzerland Co.: ca. 1 1/2 mi NW of Moorefield, 8 Sep. 1915, Deam 18811 (IND); Vermillion Co.: 2 mi S Cayuga, 2 Oct. 1936, Hermann 8446 (GH); Warren Co.: along Wabash River about 2 mi SE of Williamsport, 1 Aug. 1912, Deam 11882 (IND); Warrick Co.: 2 mi NE of Yankeetown, 2 Jul. 1915, Deam 16705 (IND); Wayne Co.: 1 mi S Williamsburg, 16 Jul. 1929, Deam 47238 (IND).

KENTUCKY: Bullitt Co.: Bernheim Forest, 1 Sep. 1969, Parreno 2 (KY); Caldwell Co.: Jones-Keeney Wildlife Area, 29 Aug. 1969, Athey 790 (MEM, NCU); Campbell Co.: ca. 4.5 mi SE of Alexandria, 20 Jul. 1980, Buddell 188 (KNK); Carter Co.: Carter Caves State Park, 2 Sep. 1972, Meijer s.n. (KY); Clark Co.: Jouett Creek, 16 Jul. 1955, Beckett 708 (KY); Edmonson Co.: Mammoth Cave, 1 Jul. 1938, Braun 1986 (US); Fayette Co.: Lexington, Short s.n. (NY); Franklin Co.: Rocky Branch, 22 Aug. 1932, Singer 137 (US); Garrard Co.: White Oak Creek, 21 Jul. 1956, Wharton 10367 (MEM); Grant Co.: Crittenden, 7 Aug. 1940, Braun 3273 (GH, US); Greenup Co.: "Big Woods", 3 mi from Boyd Co. Line, 5 Jul. 1937, Smith, Hodgdon, Gilbert, & McCoy 3553 (F, GH, NY, US); Harlan Co.: Big Black Mountain, Aug. 1893, Kearney 235 (F, MIN, KSC, GH, NY, OS, US, ISC, MO); Hickman Co.: 2.8 km S of Columbus, 6 Sep. 1975, Bryan 428 (MUR); Kenton Co.: Banklick Creek, 26 Aug. 1837, Lea s.n. (PH); Menifee Co.: below Sky Bridge in the Red River Gorge, 21 Jul. 1969, Conrad 501 (NCU, TENN); Mercer Co.: between

High Bridge and Shakertown, 23 Jul. 1955, Wharton 9205 (MEM); Nelson Co.: Bernheim Forest, 18 Sep. 1955, Gunn 520 (DHL); Oldham Co.: Harmony Landing, 10 Aug. 1956, Matthews 520 (DHL); Powell Co.: Whittleton Creek, 16 Sep. 1975, Varner 10130 (MEM); Rowan Co.: ca. 4.5 mi S of Morehead, 8 Nov. 1985, Thieret 56266 (KNK); Trigg Co.: Hematite Lake, 20 Jul. 1975, Athey 3159 (MEM, VDB); Woodford Co.: Brushy Run, 15 Jun. 1955, Wharton 8948 (MEM).

MISSOURI: Cape Girardeau Co.: Juden estate off Hwy 74, 8 Sep. 1974, Brooks 7571 (KANN, DUR); Christian Co.: Swan Creek, 3 1/2 - 4 mi SE of Chadwick, 6 Jul. 1937, Steyermark 23037 (F, NY, OS, ISC, MO, MUHW, DAO, WIS); Ozark Co.: 1 1/2 mi SW of Dugginsville, 28 Sep. 1949, Steyermark 69430 (F); Stone Co.: Galena, 8 Jun. 1914, Palmer 5894 (US, MO); Taney Co.: 6-7 mi SE of Cedar Creek, 30 Sep. 1949, Steyermark 69475 (MO).

OHIO: Adams Co.: ca. 2 mi E of Peebles, 4 Jul. 1973, Keil & Roberts 3794 (KNK); Athens Co.: near N city limits of Athens, 23 Oct. 1953, Boyce 1822 (BHO); Auglaize Co.: N of St Mary's, 17 Oct. 1903, Wetzstein 841 (MU); Butler Co.: Wester College Campus, 4 Sep. 1982, Werth OX26b49 (MU); Clermont Co.: 2 mi SSW Afton, 26 Jun. 1981, Brandenburg 786 (MU); Franklin Co.: Elk's Golf Course, 15 Aug. 1936, Blaydes s.n. (OS); Gallia Co.: rt 233, 1/2 mi SE of Gallia, 3 Sep. 1967, Herrick s.n. (OS); Greene Co.: Glen

Helen, 23 Aug. 1963, Anliot 378 (OS); Hamilton Co.: Spring Grove, 28 Aug. 1905, Braun s.n. (CINC, US); Highland Co.: Fort Hill, 13 Oct. 1952, Braun s.n. (US); Hocking Co.: Laurel Twp., 23 Jul. 1931, Bartley & Pontius s.n. (OS); Jackson Co.: Liberty Twp., 27 Sep. 1936, Bartley & Pontius 154 (NY); Lawrence Co.: Elizabeth Twp., 10 Aug. 1962, Herrick s.n. (OS); Morgan Co.: Burr Oak Lake, 15 Sep. 1967, Silberhorn 1552 (KE); Pike Co.: Mifflin Twp., 30 Sep. 1979, Cusick 19786 (OS); Ross Co.: Chillicothe, 12 Aug. 1898, Kellerman s.n. (OS); Scioto Co.: 1.3 mi SW of South Webster, 10 Aug. 1962, Herrick s.n. (OS); Vinton Co.: Lake Alma State Park, 30 Jun. 1965, O'Dell 866 (BHO); Warren Co.: Fort Ancient, 29 Aug. 1926, Roads s.n. (OS).

OKLAHOMA: LeFlore Co.: Rich Mt., just W of Arkansas border, 26 Aug. 1968, Means 3974 (OKLA); McCurtain Co.: 1.75 mi SW of Smithville, 21 Jun. 1977, Taylor 24665 (KANU, DUR).

TENNESSEE: Cheatham Co.: Pegram, 23 Jul. 1939, Svenson 10376 (BKL, WIS, SMU, DUKE, MUHW, US, TENN, GH, NY, PH, MO); Franklin Co.: 7 Jun. 1897, Eggert s.n. (US, MO); Grundy Co.: Savage Gulf Natural Area, 7 Jun. 1977, Phillippe & Patrick 3850 (TENN); Marion Co.: Speegle's Sink, near mouth of Gizzard Cove, 12 Aug. 1964, Clark & Ramseur 1120 (NCU); Montgomery Co.: 3 mi ESE of Clarksville, 24 Aug. 1947, Clebsch s.n. (US, NLU, APSC);

Rutherford Co.: 1.9 mi NE of Rockvale, 31 Jul. 1962, Franklin, Freeman, & Channell 283 (VDB); Sevier Co.: 1/4 mi S of Thorngrove Pike, 30 Aug. 1972, Hattaway s.n. (TENN, VDB); Sumner Co.: Pearson Hollow, S of Westmoreland, 1 Jul. 1975, Alcorn 667 (VDB); Warren Co.: ca. 4.6 mi ESE of Viola, 27 Jun. 1979, Patrick & Whitten 2621 (DUR); Wilson Co.: Lebanon State Park, 11 Dec. 1955, DeSelm 988 (TENN).

VIRGINIA: Bath Co.: Rough Mountain, Ca. 5 mi SW of Nimrod Hall, 23 Jun. 1982, Wieboldt 4358 (CM); Carrol Co.: 4 mi S of Ivanhoe, 14 Jul. 1936, Benedict 3533 (VPI, US); Lee Co.: 2 mi SSW of Jonesville, 24 Sep. 1985, Wieboldt & Wieboldt s.n. (VPI); Patrick Co.: Pinnacles of Dan, 2 Nov. 1973, Stevens 8241 (FARM); Russell Co.: near Castlewood, 25 Sep. 1976, Harvill 33958 (FARM); Scott Co.: ca. 3 mi W of Dungannon, 8 Aug. 1985, Wieboldt & Wieboldt s.n. (VPI).

WEST VIRGINIA: Fayette Co.: near Stretchers Neck Tunnel, 27 Aug. 1972, Grafton & McGraw s.n. (WVA); Monongalia Co.: Morgantown, 5 Jul. 1892, Nuttall s.n. (US); Munroe Co.: Chocolate Drop, 25 Jul. 1930, Berkley 1260 (MO); Upshur Co.: Ours Mill, 15 Aug. 1946, Grose s.n. (WVA); Wayne Co.: Buffalo Creek, 14 Jun. 1938, Plymale 546 (US, WVA).

CHAPTER 2

MODIFIED CARYOPSES IN POACEAE

Abstract

Scanning electron microscopy reveals that *Crypsis*, *Dactyloctenium*, *Diarrhena*, *Eleusine*, *Sporobolus*, and *Zizaniopsis* (Poaceae) produce atypical caryopses in which the pericarp is free or partially free from the seed coat. In *Sporobolus* and *Crypsis*, the pericarp becomes free from the seed coat upon moistening. The pericarp is thin and papery in both *Eleusine* and *Dactyloctenium*; in the latter the pericarp dehisces to release the seed at maturity. The pericarp in *Diarrhena* is loosely adherent to the seed coat and easily removed. The caryopsis of *Zizaniopsis* is asymmetrically inflated and achene-like.

The caryopsis -- a dry, indehiscent, one-seeded fruit with the pericarp wholly adherent to the seed coat -- is typically cited as the fruit type characteristic of the Poaceae. However, other fruit types occur in the Bambusoideae (Calderón and Soderstrom, 1980), and the pericarp is also free, loose, or non-fused in a few non-bambusoid grasses. Sporobolus, referred to as "dropseed" because of this trait, has been the most widely cited example (e.g., Cronquist, 1981). This paper reports the results of a comparative morphological study of six of the non-bambusoid grasses with loose pericarps, using scanning electron microscopy (SEM).

Prior to the nineteenth century, the grain of grasses was regarded as a bare seed (Kaden, 1961a). Richard (1808) coined the term caryopsis, and characterized it as a fruit in which the wall of the ovary is wholly attached to the integument of the seed. True (1893) reported that the single ovule of maize (Zea mays), wheat (Triticum aestivum), and oat (Avena sativa) is bitegmic, and after fertilization the outer integument and inner cell layer of the ovary wall are resorbed. During maturation, the inner integument is compressed and at maturity, it is "soldered" to the pericarp. He also noted that the outer epidermis of the nucellus persists to maturity in a compressed state.

In wheat, two cuticles are visible in cross-sections of the mature caryopsis coat: a thick outer cuticle derived from the inner integument and a thin inner cuticle from the outer epidermis of the nucellus (Fahn, 1974). Seed coat traditionally has been applied only to structures derived from the integuments (in this case, the outer cuticle), but some authors have used this term to refer to both the inner and outer cuticles (Morrison and Duschnicky, 1982). Regardless of the exact definition, the term seed coat is in widespread use with respect to the caryopsis and will be retained hereinafter, even though some authors, Bhatnagar and Chandra (1976), maintain that this cuticular region does not constitute a true seed coat.

The developmental pattern described by True (1893) is predominant among the caryopses that have been studied (Rost, 1973; Rost and Lersten, 1973), but occasional minor modifications have also been reported. In *Pennisetum americanum* (as *P. typhoideum*) only a few cells of the inner integument near its point of insertion become cutinized and persist (Narayanaswami, 1953), and in *Poa pratensis* and *Poa compressa* the outer integument persists in the mature caryopsis as a suberized layer (Andersen, 1927). However, a few genera of grasses are known to possess more extensively modified caryopses. Guérin (1898, 1899) briefly described six: *Crypsis*, *Dactyloctenium*, *Diarrhena*, *Eleusine*, *Sporobolus*, and *Zizaniopsis*. He considered

Crypsis, *Sporobolus*, and *Diarrhena* to possess true caryopses, but with peculiar pericarps; *Eleusine* and *Dactyloctenium* he described as achene-like but with thin walls; and he believed that *Zizaniopsis* fruits represented true achenes.

MATERIALS AND METHODS - I examined the fusion of pericarp and seed coat in *Crypsis*, *Dactyloctenium*, *Diarrhena*, *Eleusine*, *Sporobolus* and *Zizaniopsis*. *Dactylis* and *Triticum* were employed as controls. Caryopses were selected from herbarium specimens of *Crypsis schoenoides* (*Farwell*, *1253*: OKL), *Dactylis glomerata* (*Bailey and Swayne*, *1412*: OKL), *Dactyloctenium aegyptium* (*Ahles* and *Leisner*, *32441*: NCU), *Diarrhena americana* var. *obovata* (*Anderson*, *1072*: ISC), *Eleusine indica* (*Zanoni*, *3699*: OKL), *Sporobolus giganteus* (*Rice*, *s.n.*: OKL), *Triticum aestivum* (*Merkel*, *s.n.*:OKL), and *Zizaniopsis miliacea* (*Waterfall*, *7627*: OKL). Cross-sections of *Crypsis*, *Dactylis*, *Diarrhena*, *Sporobolus*, *Triticum* and *Zizaniopsis* were cut with a razor blade. All materials were mounted on metal stubs via double-stick tape, and coated with gold-palladium. Selected caryopses of *Crypsis* and *Sporobolus* were moistened with water for 2-3 min and observed under a dissecting microscope. One cross-section of *Sporobolus* was moistened with a drop of water after being mounted on the stub, but prior to being metal-coated for SEM. Portions of the walls of the caryopses of *Diarrhena* and *Zizaniopsis* were mechanically removed prior to mounting. Specimens were viewed in an ETEC Autoscan scanning electron microscope at an accelerating voltage of 20 kV and a working distance of 20-25 mm.

Caryopses of *Zizaniopsis* were experimentally submersed in water for 30 days to test for flotation.

RESULTS AND DISCUSSION - The precise limits of the seed coat in mature caryopses is difficult to discern, as noted by Fahn (1974) for wheat. A distorted layer, however, presumably reflects the developmental forces that led to fusion (Fig. 1, 2). The caryopsis of orchard grass (*Dactylis glomerata*) (Fig. 3) does not differ in any significant detail from that of wheat, the pericarp being wholly fused to the seed coat (Fig. 4). Wheat and orchard grass are illustrated to demonstrate the degree of pericarp-seed coat fusion characteristic of true caryopses.

Among the atypical caryopses employed in this study, I recognize four groups:

Sporobolus type

This group includes both *Sporobolus* (Fig. 5-8), and *Crypsis* (Fig. 9-11). The caryopsis of *Sporobolus giganteus* (Fig. 5) has a thick pericarp closely investing, but apparently free from, the seed (Fig. 6). When submersed in water for 2 or 3 min, the seed is extruded through a slit that opens along one side of the pericarp (Fig. 7). *In situ*, these seeds often emerge but remain partially attached to the mucilaginous pericarp (Fig. 8). A similar situation was observed in *Crypsis schoenoides* (Fig. 9-11), and Arber (1934) noted that the shiny seeds of *Crypsis aculeata* may be found covering the panicles after heavy rains.

Eleusine type

In the caryopses of *Eleusine indica*, the pericarp appears in SEM as a papery membrane, loosely investing and free from the seed coat (Fig. 12, 13). The mature seeds are either wholly enveloped in this thin pericarp (Fig. 12) or sometimes have only tattered remnants of the pericarp. The mature seed coat is highly sculptured and hard (Fig. 14). This coat is developed from the inner integument; the inner and middle layers of the pericarp collapse (Cummins, 1929; Narayanaswami 1955; Chandra, 1963). The caryopses of *Dactyloctenium aegyptium* (Fig. 15) follow a similar developmental pathway to those of *Eleusine indica* (Chandra, 1963) except that at maturity the seed is released from the ruptured pericarp (Fig. 16).

Diarrhena type

The pericarp of the caryosis of *Diarrhena americana* var. *obovata* is mostly free from the seed coat. Where free, the pericarp is thicker than in regions of fusion. In Fig. 17, a portion of the pericarp of this caryopsis has been peeled away using a fingernail. The loose association between the pericarp and the seed coat can be seen in a cross-section (Fig. 18). In *Diarrhena japonica* and *D. mandschurica*, the pericarp is not as thick as that of *D. americana* var. *obovata*, but the caryopses are otherwise developmentally and morphologically similar (Guérin, 1899; Schwab, 1971).

Zizaniopsis type

The last group is typified by southern wild rice (*Zizaniopsis miliacea*). The asymmetrical, long-beaked caryopses of this species have thick but fragile walls with a sclerified outer pericarp (Guérin, 1898) (Fig. 19). A cross-section of the caryopsis reveals that the pericarp is fused to the seed coat only near the base (Fig. 20, 21).

On the basis of their resemblance to fruit types other than the true caryopsis, various terms have been employed to describe these grass fruits: (1) utricle -- *Crypsis*, *Dactyloctenium*, *Eleusine*, and *Sporobolus*; (2) achene - *Dactyloctenium*, *Eleusine*, and *Zizaniopsis*; (3) nut or nutlike - *Eleusine* and *Zizaniopsis*; (4) saccular - *Crypsis*, *Eleusine*, and *Sporobolus* (Allen, 1980; Arber, 1934; Chandra, 1963; Guérin, 1898; Hackel, 1890; Narayanaswami, 1955; Roshevits, 1937; Terrel and Robinson, 1974). Kaden (1961a,b), in rejecting these and other terms such as "pseudocaryopsis", pointed out the overall developmental and morphological similarity between these specialized grass fruits and the true caryopsis: both are formed from a superior, unilocular, compound ovary; possess a solitary, bitegmic ovule; have a similar specialized embryo-type; and exhibit the same relative position of embryo and endosperm. I conclude that the presence of a free or partially free pericarp in these six grasses is the result of evolutionary modification of the true caryopsis. I believe it is preferable to refer to these fruits as modified caryopses, rather than by the use of other terms from the decidedly artificial classification of fruit types.

Although it is possible to speculate about potential selective advantages or functions for modifications of the true caryopsis, I have evidence for only two of the types, both related to dispersal. The air-space between the free pericarp and seed in the caryopses of Zizaniopsis allows for their buoyancy in water, thereby permitting an effective means of dispersal for this aquatic species. Submersed mature caryopses from herbarium specimens immediately floated to the surface, and floated for 30 days, after which time the experiment was terminated. Floating fruits have also been observed in native populations of southern wild rice. In the Sporobolus type, mucilage from the gelatinous pericarps is transferred to the seeds, permitting them to adhere to passing animals; later upon drying, the seeds fall to the ground (Bor, 1960).

Non-bambusoid grass genera with modified caryopses occur primarily in two subfamilies (Table 1), the Oryzoideae and the Chloridoideae.

Both Luziola (including Hydrochloa) and Zizaniopsis have been included within the small subtribe Luziolinae

(Oryzoideae) (Terrell and Robinson, 1974), and it is likely that their similar fruits have resulted from a single evolutionary modification.

The relationships among the genera within the subfamily Chloridoideae are more complex. In part this results because the boundaries between the tribes within this subfamily are problematical (Stebbins and Crampton, 1961). The similar, but unusual caryopses of Sporobolus and Crypsis (including Heleochloa), in addition to other shared morphological features between these genera, would indicate a common origin for these fruits. A pericarp that becomes free upon moistening has been reported for Calamovilfa longifolia (Reeder and Ellington, 1960), and the descriptions and illustrations of Urochondra setulosa (Bor, 1960) also place this grass in the Sporobolus type of modified caryopsis.

Acrachne, Dactyloctenium, and Eleusine were united into a single cluster in a cluster analysis, and appear to be closely related (Hilu and Wright, 1982). The caryopsis type found within these three genera is therefore likely to be the result of a shared evolutionary modification.

In his analysis of the subfamilies and tribes of Poaceae in the southeastern United States, Campbell (1985) discussed the inconsistent and often arbitrary characters that have been used to define the tribes in the

Chloridoideae. As a result he united several tribes into one, the Cynodonteae, which includes, among others, *Calamovilfa*, *Crypsis*, *Dactyloctenium*, *Diplachne*, *Eleusine*, *Leptochloa*, *Muhlenbergia*, and *Sporobolus*. In his discussion of the relationships among these genera and the circumscription of tribes within the subfamily, caryopsis type is not mentioned. Clayton (1978), among the few authors to have formally segregated a tribe Sporoboleae, did so on the basis of possession of single-flowered spikelets, thereby including *Muhlenbergia*, which has typical caryopses. I believe that the Sporobolus type of caryopsis represents a synapomorphy, and this should be reflected by the recognition of a separate tribe or subtribe for those grasses with this caryopsis type: *Calamovilfa*, *Crypsis*, *Sporobolus*, and *Urochondra*. *Acrachne*, *Dactyloctenium*, and *Eleusine* should similarly be treated in their own tribe or subtribe.

Diarrhena, *Phaenosperma*, and *Psammochloa* are problematic with respect to subfamilial classification. Although attempts have been made to place *Diarrhena* within the Cynodonteae (Chloridoideae) on the basis of the loose pericarp, such an association is not supported by a preponderance of morphological and anatomical evidence (Macfarlane and Watson, 1980). Macfarlane and Watson (1980) have made suggestions as to the affinities of these three genera: *Diarrhena* - oryzoid or bambusoid;

Phaensoperma - arundinoid, bambusoid, oryzoid, or centostecoid; *Psammochloa* - Stipeae.

Although more detailed developmental analyses need to be completed before evolutionary patterns can be fully ascertained, it would appear that loose pericarps have arisen independently on several occasions, even within the Chloridoideae, and they may be useful in assessing suprageneric relationships.

LITERATURE CITED

ALLEN, C. M. 1980. Grasses of Louisiana. Univ. of Southwestern Louisiana, Lafayette.

ANDERSEN, A. M. 1927. Development of the female gametophyte and caryopsis of *Poa pratensis* and *Poa compressa*. J. Agric. Res. 34:1001-1018.

ARBER, A. 1934. The Gramineae: A study of cereal, bamboo, and grass. Cambridge Univ. Press, New York.

BEWS, J. W. 1929. The world's grasses: Their differentiation, distribution, economics and ecology. Longmans, Green and Co., Ltd., London.

BHATNAGAR, S. P. AND S. CHANDRA. 1976. Reproductive biology of *Triticum*. V. Post-pollination development of nucellus, integuments and pericarp in relation to time. Phytomorphology 26:139-143.

BOR, N. L. 1960. The Grasses of Burma, Ceylon, India and Pakistan. Pergamon Press, New York.

CALDERÓN, C. E. AND T. R. SODERSTROM. 1980. The genera of Bambusoideae (Poaceae) of the American continent: Keys and comments. Smithsonian Contr. Bot. 44:1-27.

CAMPBELL, C. S. 1985. The subfamilies and tribes of Gramineae (Poaceae) in the southeastern United States. J. Arnold Arbor. 66:123-199.

CHANDRA, N. 1963. Morphological studies in the Gramineae. IV. Embryology of Eleusine indica Gaertn. and Dactyloctenium aegyptium (Desf) Beauv. Proc. Indian Acad. Sci. 58:117-127.

CLAYTON, W. D. 1978. Gramineae in: Heywood, V. H. (ed.) Flowering plants of the world. Mayflower Books, New York.

CRONQUIST, A. 1981. An integrated system of classification of flowering plants. Columbia Univ. Press, New York.

CUMMINS, M. P. 1929. Development of the integument and germination of the seed of Eleusine indica. Bull. Torrey Bot. Club 56:155-162.

FAHN, A. 1974. Plant anatomy, 2nd ed., Pergamon Press, Oxford.

GUÉRIN, M. P. 1898. Structure particulière du fruit de quelques Graminées. Jour. de Bot. 12:365-374.

_______. 1899. Recherches sur le développement du tégument séminal et du péricarpe des Graminées. Ann. Sci. Nat. Bot. 9:1-64.

HACKEL, E. 1890. The true grasses. Translated from Die naturlichen Pflanzenfamilien by F. Lamson-Scribner and E.A. Southworth. Henry Holt and Co., New York.

HAMMEL, B. E. AND J. R. REEDER. 1979. The genus *Crypsis* (Gramineae) in the United States. Syst. Bot. 4:267-280 .

HILU, K. W. AND K. WRIGHT. 1982. Systematics of Gramineae: a cluster analysis study. Taxon 31:9-36.

KADEN, N. N. 1961a. Caryopsis as the main fruit type in grasses. Morfogenes Rastenii 2:307-310. Moscow Univ. Press, Moscow (in Russian).

_______. 1961b. Subtypes of the caryopsis. Morfogenes Rastenii 2:311-314. Moscow Univ. Press, Moscow (in Russian).

MACFARLANE, T. D. AND WATSON, L. 1980. The circumscription of Poaceae subfamily Pooideae, with notes on some controversial genera. Taxon 29:645-666.

MORRISON, I. N. AND L. DUSHNICKY. 1982. Structure of the covering layers of the wild oat (*Avena fatua*) caryopsis. Weed Sci. 30:352-359.

NARAYANASWAMI, S. 1953. The structure and development of the caryopsis in some Indian millets. 1. *Pennisetum typhoideum* Rich. Phytomorphology 3:98-112.

_______. 1955. The structure and development of the caryopsis in some Indian millets. Annual Rep. Michigan Acad. Sci. 40:33-46, pl. 1-3.

REEDER, J. R. AND M. A. ELLINGTON. 1960. Calamovilfa, a misplaced genus of Gramineae. Brittonia 12:71-77.

RICHARD, L. 1808. Demonstrations botaniques, ou analyse du fruit, considere en general. Paris.

ROSHEVITS, R. Y. 1980. Grasses: An introduction to the study of fodder and cereal grasses. Translation of 1937 work (in Russian). Indian National Scientific Documentation Centre, New Delhi.

ROST, T. L. 1973. The anatomy of the caryopsis coat in mature caryopses of the yellow foxtail grass (Setaria lutescens). Bot. Gaz. 134:32-39.

_______, AND N. R. LERSTEN. 1973. A synopsis and selected bibliography of grass caryopsis anatomy and fine structure. Iowa State J. Res. 48:47-87.

SCHWAB, C. A. 1971. Floral structure and embryolgy of Diarrhena (Gramineae). Doctoral dissertation, Iowa State University, Ames.

STEBBINS, G. L. AND B. CRAMPTON. 1961. A suggested revision of the grass genera of temperate North America. Recent Advan. Bot. 1:133-145.

TERRELL, E. E. AND H. ROBINSON. 1974. Luziolinae, a new subtribe of oryzoid grasses. Bull. Torrey Bot. Club 101:235-245.

TRUE, R. H. 1893. On the development of the caryopsis. Bot. Gaz. 18:212-227, pl. XXIV-XXVI.

WATSON, L. AND M. J. DALLWITZ. 1980. Australian grass genera. Anatomy, morphology, and keys. Australian National Univ., Canberra, Australia.

Table 1. Subfamilial distribution of genera reported as possessing modified caryopses.

SUBFAMILY	GENERA
Oryzoideae	*Luziola*[1], *Zizaniopsis*
Chloridoideae	*Acrachne*[2], *Blepharoneuron*[3], *Calamovilfa*[4], *Crypsis*, *Dactyloctenium*, *Diplachne*[2], *Eleusine*, *Leptochloa*[2], *Sporobolus*, *Thellungia*[2], and *Urochondra*[5]
unplaced	*Diarrhena*[6], *Phaenosperma*[6], and *Psammochloa*[6]

References: 1. Terrell and Robinson, 1974. 2. Watson and Dallwitz, 1980. 3. Bews, 1929. 4. Reeder and Ellington, 1960. 5. Bor, 1960. 6. Macfarlane and Watson, 1980.

Fig. 1-11. SEMs of caryopses. Fig. 1,2. *Triticum aestivum*. 1. whole caryopsis. x 8.5. 2. cross-section of caryopsis. E, endosperm; A, aleurone layer; P, pericarp. x 435. Fig. 3,4. *Dactylis glomerata*. 3. whole caryopsis. x 17.5.

4. cross-section of caryopsis. x 45. Fig. 5-8. *Sporobolus giganteus*. 5. whole caryopsis. x 35. 6. cross-section of caryopsis. arrow = fissure between pericarp and seed coat. x 250. 7. cross-section with portion of pericarp peeling away after addition of water. x 65. 8. seed emerging laterally from pericarp, *in situ*. x 25. Fig. 9-11. *Crypsis schoenoides*. 9. whole caryopsis. x 25.

10. cross-section of caryopsis. x 70. 11. seed. x 25.

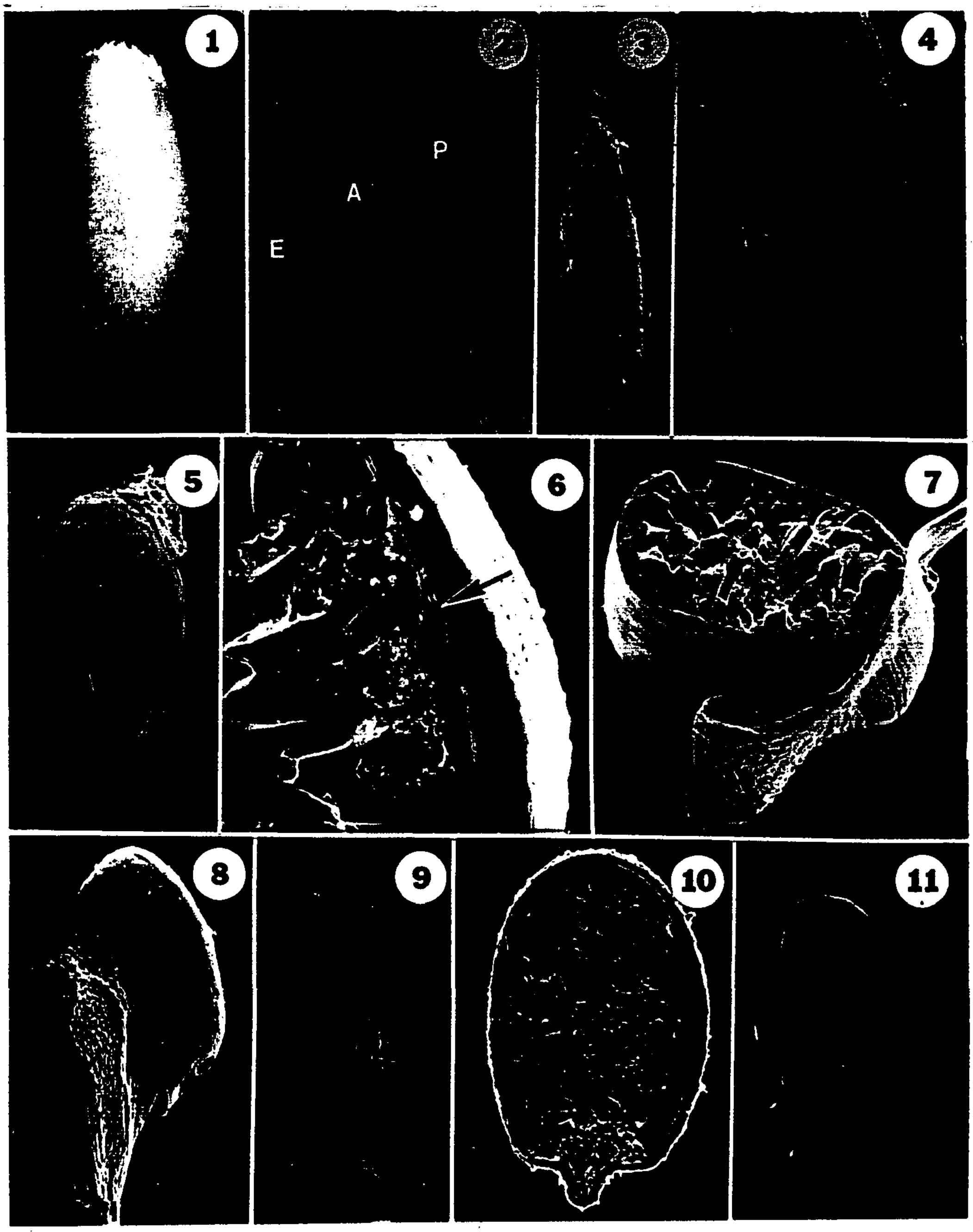

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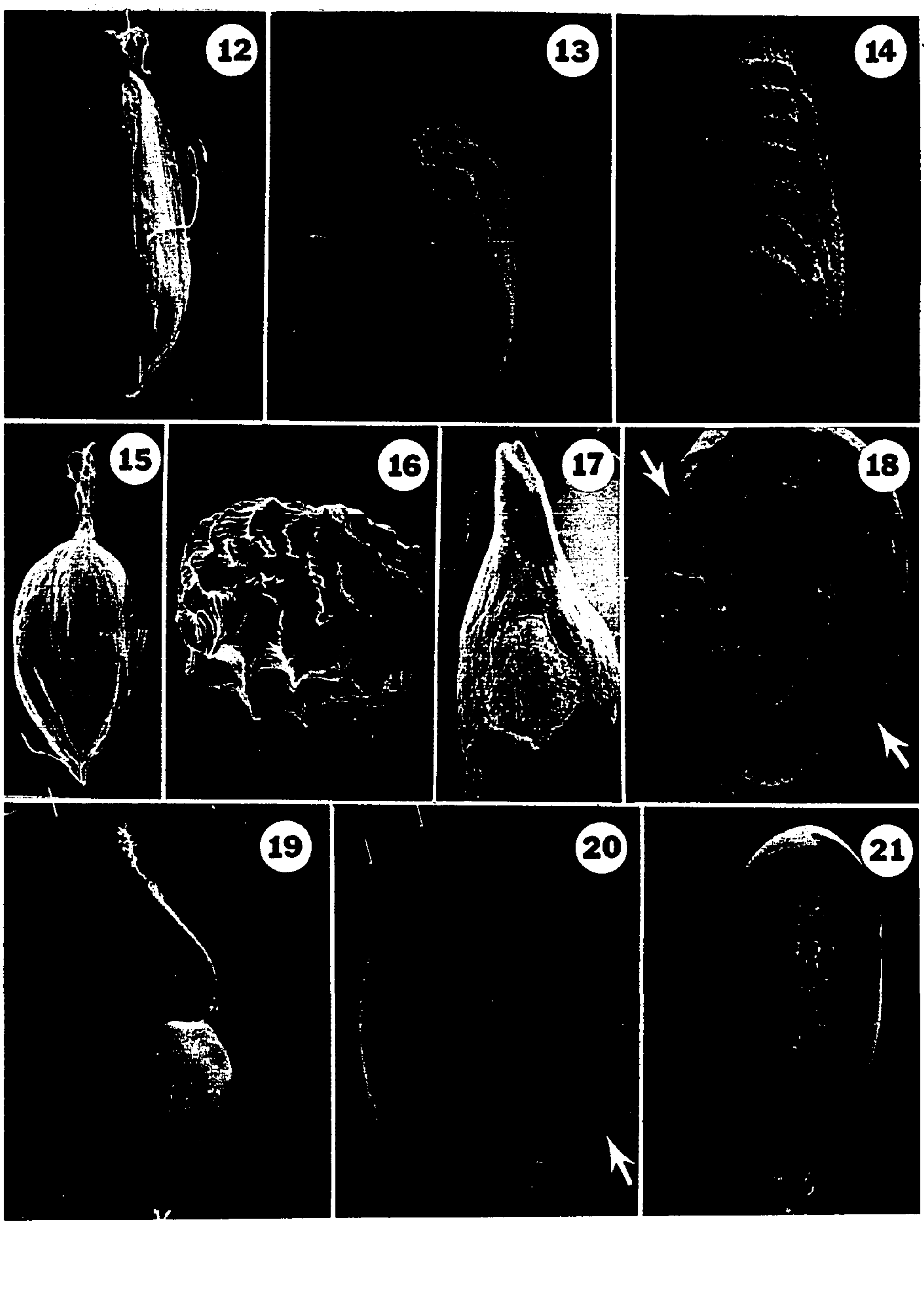
Fig. 12-21. SEMs of caryopses. Fig. 12-14. *Eleusine indica*. 12. whole caryopsis. x 25. 13. caryopsis with lower portion of pericarp mechanically removed. x 25. 14. seed. x 45. Fig. 15, 16. *Dactyloctenium aegyptium*. 15. whole caryopsis. x 30. 16. seed. x 45. Fig. 17, 18. *Diarrhena americana* var. *obovata*. 17. whole caryopsis with central portion of pericarp mechanically removed. x 10. 18. cross-section of caryopsis. arrows = fissure between pericarp and seed coat. x 25. Fig. 19-21. *Zizaniopsis milicea*. 19. whole caryopsis. x 10. 20. cross-section of caryopsis. arrow = fissure between pericarp and seed coat. x 25. 21. caryopsis after removal of beak and portion of pericarp. x 25.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CHAPTER 3

BACKSCATTERED ELECTRON IMAGING AS A TECHNIQUE FOR VISUALIZING SILICA BODIES IN GRASSES

Abstract

Patterns of silica body distribution provide useful comparative taxonomic information in the Poaceae, especially at the levels of subfamily and tribe. Principal methods currently employed to study silica bodies in grasses are light microscopy and secondary electron imaging. Preparations for light microscopy, including scraping, ashing, and staining, are time consuming and destructive of the specimen; they do not always yield optimal or easily interpreted results. Secondary electron imaging is limited to superficial siliceous structures and cannot be used to image subsuperficial silica bodies. Elemental area maps obtained by use of an energy dispersive x-ray analyzer overcome this problem, but the resolution is poor and the outlines of the silica bodies are often not clear.

Backscattered electron imaging (BEI) is an effective means of visualizing silica bodies in grass leaves. Advantages of BEI include the production of high-contrast images with sharply demarcated outlines, even for silica bodies that are subsuperficial or present in small numbers. Furthermore, destruction of the sample is not required during preparation and any dried herbarium specimen may be utilized. Penetration of the electron beam at 30 kV is

sufficient to reveal both superficial and subsuperficial silica bodies. Unequivocal images were obtained for the major types of silica bodies representative of all six subfamilies of North American Poaceae.

Introduction

Silica deposits are characteristic of several families of Liliopsida (=Monocotyledoneae) in the orders Arecales, Bromeliales, Cyperales, Poales, Restionales, and Zingiberales. Silica bodies occur, but are less common in the monocot orders Commelinales, Eriocaulales, Juncales, and Orchidales (Dahlgren and Clifford, 1982). Silica deposits occur infrequently in the Magnoliopsida (=Dicotyledoneae) and may be found in the Cannabaceae, Fabaceae, Ulmaceae, Urticaceae, and Verbenaceae (Kaufman et al., 1981). Among the flowering plants, silica bodies have been studied most extensively in the Poaceae (=grasses), where they occur in a myriad of forms.

Among the numerous methods for observing silica bodies, scanning electron microscopy (SEM) has emerged as one of the most important. Of several potentially useful signals resulting from the interaction of the primary electron beam in an SEM and the specimen sample, the backscattered electron image (BEI) is currently little used by botanists. To a first approximation, the strength of the backscattered signal depends upon the average atomic number (Z-number) of the sample area irradiated (Newbury, 1977); therefore, I investigated the utility of BEI to visualize silicon (as silica) in grass leaves.

Silica Bodies in the Poaceae

Silicon is absorbed by grasses from the soil solution as undissociated monosilicic acid, H_4SiO_4, and may accumulate in virtually any part of the plant as hydrated amorphous silica, $SiO_2 \cdot nH_2O$ (Parry and Kelso, 1975; Sangster, 1977; 1985; Salisbury and Ross, 1978; Ellis, 1979). The exact mechanism(s) by which the monosilicic acid polymerizes to form amorphous silica is not known; however, both active and passive mechanisms have been proposed (Blackman and Parry, 1968; Blackman, 1969; Kaufman et al., 1981; Sangster et al., 1983b). As yet, a direct metabolic role for this element has not been demonstrated (Lewin and Reimann, 1969; Clarkson and Hanson, 1980; Kaufman et al., 1985).

Sangster and Parry (1981) recognized three categories of silica deposits in the leaves of grasses: (1) opaline silica bodies, (2) cell wall deposits, and (3) extracellular deposits. The first of these has been most widely studied and is the focus of this report. Hydrated silica is deposited in specialized epidermal cells known as silica cells, and usually assumes the characteristic shape of the lumen (Blackman, 1971; Geis, 1978). The shapes and distribution of silica bodies in grass leaves tend to be characteristic of a given species (Blackman, 1971). The size and relative abundance of the silica bodies can be affected by various environmental factors including soil pH, availability of silicon, and tissue age, but the overall characteristic distribution and shape of the silica bodies is maintained (Sangster, 1970; Ellis, 1979). Patterns of silica body distribution provide useful comparative taxonomic information, especially at the levels of subfamily and tribe.

Silica bodies in grass leaf blades may be costal or intercostal. They occur on both surfaces but are generally studied on the abaxial surface of the blades. The adaxial suface has fewer silica bodies (Ellis, 1979) and has further disadvantages of prominent ribbing and irregularities of cell size (Clifford and Watson, 1977). Although usually found in the epidermis, silica bodies may be located in the mesophyll adjacent to vascular strands (Dahlgren and Clifford, 1982). Descriptions and classifications of silica bodies in grasses are given in Metcalfe (1960), Clifford and Watson (1977), and Ellis (1979).

Gould and Shaw (1983) and Watson and Dallwitz (1980) provided descriptions of the silica bodies that characterize subfamilies and tribes of United States and Australian grasses, respectively. The most complete account of the different types found in genera and species of grasses is given by Metcalfe (1960). Each of the North American subfamilies of grasses is typified by characteristic silica body types (Table 1). Following the decomposition of the surrounding organic tissues, silica bodies persist in the soil as opaline (opal) phytoliths (Sangster and Parry, 1981) and provide useful data for archaeological, paleogeographical, and paleoecological research (Brown, 1984; Pearsall and Trimble, 1984). Twiss et al. (1969) developed a brief classification scheme for phytoliths, and Brown (1984) wrote an extensive key with illustrations for the identification of opal phytoliths.

Materials and Methods

Pieces of dried leaf blades were removed from herbarium specimens and mounted on metal stubs using silver paint. Both adaxial and abaxial sections from the same specimen were mounted on a single stub, and the surface that afforded the better view of silica bodies (usually abaxial) was utilized. Although overall distribution of silica bodies may differ, the pattern of distribution in a species is characteristic; therefore no distinction is made in the present report between abaxial and adaxial surfaces.

The specimens were coated with carbon in a JEOL vacuum evaporator to permit later use for x-ray analysis. One specimen (*Isachne*) was coated with gold-palladium to evaluate the effect of metal coating in conjunction with BEI. Specimens were viewed in an ETEC Autoscan scanning electron microscope. To be certain that a particular structure contained silicon, qualitative elemental analysis was performed with the use of a PGT Model III energy dispersive x-ray (EDX) analyzer. This information was displayed graphically by elemental area maps, line scans, and spectrum histograms. Backscattered electrons were detected by a solid state G-W Electronics BEI detector, using an accelerating voltage of 30 kV. A working distance of 15 mm was optimal.

Characteristic silica bodies of the different subfamilies are illustrated following the convention of Metcalfe (1960) wherein the longitudinal axis of the leaf is viewed horizontally, except as noted. Herbarium specimens of grasses used in this study are as follows: *Avena sativa*: Ellis Co., Oklahoma (OKL:28867); *Bouteloua hirsuta*: Woodward Co., Oklahoma (OKL:53308); *Isachne pallens*: Oahu, Hawaii (OKL:50487); *Oryza sativa*: McCurtain Co., Oklahoma (OKL:61835); *Pariana* sp.: Para, Brazil (MO:2399851); *Phragmites australis*: McClain Co., Oklahoma (OKL:59892); *Schizachyrium scoparium*: Cleveland Co., Oklahoma (OKL:60717); *Sorghum halepense*: Bryan Co., Oklahoma (OKL:62202). Herbarium abbreviations follow Holmgren et al. (1981).

Results

Silica bodies of *Oryza sativa*, as viewed in secondary electron imaging (SEI) in the SEM, are indicated in Figure 1 with a superimposed x-ray scan for the Si window. The straight line at the center of the field indicates the location of the scan; the variable line above represents relative intensity of the Si signal during a single horizontal scan. Silica is deposited in abundance in *Oryza*, making this taxon unusually well-suited for SEI. An accompanying x-ray spectrum confirmed the siliceous nature of these deposits (Fig. 2) and also the presence of low levels of several biologically active elements, including calcium, potassium, and chlorine, which were present in the dried specimen.

Other grass leaves may have less easily observed silica bodies in SEI, as exemplified by *Schizachyrium* (Fig. 3a). The subsurface dumbbell-shaped silica bodies were scarcely visible via SEI. A matching elemental dot map of the Si x-ray signal in Fig. 3b illustrated the location of x-ray signals in the range of 1.66 to 1.81 keV. The shape of the silica bodies, although evident, was poorly resolved. In contrast, BEI used on the same sample (Fig. 3c) clearly indicated the location, size, and shape of the silica bodies. Because of its annular design, the BEI detector also is not as sensitive to orientation as is the x-ray detector (compare Figs. 3b and 3c).

The applicability of this technique for representatives of all six subfamilies of North American grasses is demonstrated in Figure 4. In each of these, the small content of elements near or above the Z-number of Si did not affect the shape or orientation of the silica bodies as seen in BEI. Further, the presence of small concentrations of such biologically common elements as potassium, calcium, and chlorine could help to accentuate the location of cellular structures by their differential distribution in dried tissue. This may provide a clear image of the background tissue but permits silica bodies to be distinguished.

A specimen of *Isachne* was coated with gold-palladium in order to assess whether material prepared by conventional means for SEI could be studied by BEI. The image of the metal-coated specimen was of acceptable quality and nearly equivalent to that of the carbon-coated specimens (Fig. 4g). Apparently, the thicker dimension of silica bodies and the generation of numerous, deeper, backscattered primary electrons provided a significantly stronger signal than the heavier atomic numbers of the coating elements. Therefore, metal-coating of grass specimens for BEI may be employed with satisfactory results if carbon-coated material is not available.

Discussion

Numerous methods have been employed to visualize silica bodies in grass leaves, most of which require extensive treatment of the organ examined and destruction or alteration of surrounding tissues. One of the most common methods involves removing the adaxial epidermis and mesophyll by scraping with a razor blade until only the abaxial epidermis remains (Shaw and Smeins, 1981). With this technique it is difficult to remove all the mesophyll cells that may obscure the epidermis, and therefore, alternative methods to remove unwanted leaf material have also been developed. Chemical treatments have been used to digest the surrounding leaf material ("wet ashing"), and these may involve the use of (a) strong oxidizing agents, e.g., hydrogen peroxide (Parry and Smithson, 1958; 1964), (b) strong acids, e.g., chromic acid (Parry and Hodson, 1982), (c) strong bases, e.g., sodium or potassium hydroxide (Sangster et al., 1983a; 1983b) or (d) various combinations of these reagents. One week of treatment may be required to prepare some specimens (Parry and Smithson, 1958); damage from these harsh treatments often obscures spatial relationships among epidermal cells. "Dry ashing" involves the use of high temperatures instead of chemicals. In order to keep the overall depositional pattern in the epidermis intact, materials have been placed between glass slides before subjecting them to 500^{o}C heat in a furnace.

The upper slide can then be removed and mounting medium added directly to the ash, followed by a coverslip (Lanning et al., 1980). Silica bodies are generally viewed with light microscopy by either mounting in a medium of suitable optical density or by utilizing interference optics for enhancement of the image (Sangster and Parry, 1981). Staining procedures involving silver-amine chromate, methyl red, and crystal violet lactone may be used to localize silica (Dayanandan, 1983; Dayanandan et al., 1983). However these reagents are not specific for silica, and interfering components must first be removed by treatment with acids (Kaufman et al., 1985). Often silica bodies are not in a single plane of focus for light microscopy, therefore making accurate descriptions more difficult.

Transmission electron microscopy has been used to investigate the ultrastructural development of cork-silica pairs (Kaufman et al., 1970; Lawton, 1980) and silicification in reproductive bracts (Hodson et al., 1984; 1985). Of wider application for the study of silica bodies is scanning electron microscopy using secondary electron imaging. Through the use of SEI, silica bodies may be seen in surface view (Palmer and Tucker, 1981; 1983) and analyzed with an EDX device to give an elemental area map (Fig. 3b) or x-ray line scan (Fig. 1) of siliceous structures *in situ*. The latter two techniques, however, have considerably lower resolution than either BEI or SEI.

Examples of the use of SEI to study silica in grasses can be found in the studies of *Phragmites* (Lau et al., 1978) and *Leersia* and *Zizania* (Terrell and Wergin, 1979; 1981; Terrell et al., 1983). The greater resolution of SEI makes it an ideal choice for silica bodies with an externally visible contour. However, SEI is inadequate for imaging subsurface silica bodies (Fig. 3a).

The electron-probe analyzer has provided a means to assay silicon quantitatively (Kaufman et al., 1969; Hayward and Parry, 1973; Sangster, 1977; Sangster et al., 1983a; Gartner et al., 1984). Takeoka and colleagues used soft x-rays to ascertain the distribution and relative frequency of silica bodies in rice plants (Takeoka et al., 1983; 1984). Less frequently used methods to study silica in higher plants include atomic absorption spectroscopy, infrared spectroscopy, liquid scintillation counting, mass spectroscopy, and neutron activation analysis (Kaufman et al., 1981).

Backscattered Electron Imaging

Backscattered electrons were first detected as early as 1953 (Wells, 1977). They result from interaction of the electrons in the primary beam and the nuclei of atoms of the specimen (DeNee and Abraham, 1976). This electron-nucleus interaction is referred to as an elastic event, in contrast to the electron-electron (inelastic) events that result in formation of secondary electrons. Elastic collisions result in relatively little loss of energy, and thus backscattered electrons have considerably more energy than secondary electrons. Backscattered electrons travel in nearly straight lines, and the signal originates from deeper in the specimen than does the signal formed from secondary electrons. As the Z-number of the sample increases, more backscattered electrons of higher energy are produced because of the growing importance of elastic relative to inelastic collisions (Becker and Sogard, 1979). In addition to atomic number, the backscattered electron signal also depends upon topography (Robinson, 1975), which must be taken into account when optimizing the signal. Current solid state backscattered-electron detectors respond only to electrons with a specific energy threshold value; therefore, lower energy secondary electrons are not detected (Ball and McCartney, 1981).

The principal use of BEI to date has been in metallurgy, where Z-number contrast has been used to discriminate among the individual components in alloys (e.g., Price and Johnson, 1971). Naturally occurring Z-number contrast, although less exploited in biology, has been employed to image bone calcifications, toxic exposure to metals, and particulate matter in the lungs (Abraham and DeNee, 1974; Craighead and Vallyathan, 1980). Biological applications of BEI have more frequently involved the use of heavy metal stains (silver or osmium salts) to impart Z-number contrast selectively to biological tissues. The surface of a structure may therefore be viewed by secondary electron imaging, and BEI can be used simultaneously to visualize subsuperficial structures (Becker and Sogard, 1979). The major limitation to BEI is its relatively lower resolution (100 Å) using conventional microscopes; however, this is unlikely to be detrimental in survey work on grass silica bodies.

Backscattered electron imaging proved to be advantageous in visualizing silica bodies in grasses (Fig. 4). This resulted because the atomic number contrast of silicon renders these structures easily visible, even if present in low numbers. The greater depth of field of BEI allowed siliceous structures to be observed in one plane of focus. Furthermore, destruction of the sample was not required during preparation, and therefore herbarium specimens could be utilized. Backscattered electron imaging proved capable of resolving subsurface silica deposits (Fig. 3c) and further provided for extremely high contrast between siliceous structures and surrounding leaf materials. Elemental area maps of subsuperficial silica bodies may be obtained through use of an energy dispersive x-ray analyzer (Fig. 3b), but for descriptive purposes, these images are inferior to the sharply demarcated outlines produced with BEI (Fig. 3c). The results of my study demonstrate that

BEI is an effective tool to aid in visualizing silica bodies in grasses in the context of surrounding tissues.

References

Abraham JL, DeNee PB. (1974) Biomedical applications of backscattered electron imaging--one year's experience with SEM histochemistry, Scanning Electron Microsc. 1974: 252-258.

Ball MD, McCartney DG. (1981) The measurement of atomic number and composition in an SEM using backscattered detectors, J. Microscopy, 124, 57-68.

Becker RP, Sogard M. (1979) Visualization of subsurface structures in cells and tissues by backscattered electron imaging, Scanning Electron Microsc. 1979; II:835-870.

Blackman E. (1969) Observations on the development of the silica cells of the leaf sheath of wheat (*Triticum aestivum*), Can. J. Bot. 47, 827-838.

Blackman E. (1971) Opaline silica bodies in the range grasses of southern Alberta, Can. J. Bot. 49, 769-781.

Blackman E, Parry DW. (1968) Opaline silica deposition in rye (*Secale cereale* L.), Ann. Bot. 32, 199-206.

Brown DA. (1984) Prospects and limits of a phytolith key for grasses in the central United States, J. Archaeological Sci. 11, 345-368.

Clarkson DT, Hanson JB. (1980) The mineral nutrition of higher plants, Ann. Rev. Plant Physiol. 31, 239-298.

Clifford HT, Watson L. (1977) Identifying Grasses: data, methods and illustrations, Univ. of Queensland Press, St. Lucia, Australia, 39-41.

Craighead JE, Vallyathan NV. (1980) Cryptic pulmonary lesions in workers occupationally exposed to dust containing silica, J. Amer. Med. Assoc. 244, 1939-1941.

Dahlgren RMT, Clifford HT. (1982) The Monocotyledons: A Comparative Study, Academic Press, NY, 87-90.

Dayanandan P. (1983) Localization of silica and calcium carbonate in plants, Scanning Electron Microsc. 1983; III:1519-1524.

Dayanandan P, Kaufman PB, Franklin CI. (1983) Detection of silica in plants, Amer. J. Bot. 70, 1079-1084.

DeNee PB, Abraham JL. (1976) Backscattered electron imaging, in Principles and Techniques of Scanning Electron Microscopy, M.A. Hayat (ed.), Van Nostrand Reinhold, NY, 144-180.

Ellis RP. (1979) A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view, Bothalia 12, 641-671.

Gartner S, LeFaucheur L, Roinel N, Paris-Pireyre N. (1984) Preliminary studies on the elemental composition of xylem exudate from two varieties of wheat by electron probe analysis, Scanning Electron Microsc. 1984; IV:1739-1744.

Geis JW. (1978) Biogenic opal in three species of Gramineae, Ann. Bot. 42, 1119-1129.

Gould FW, Shaw RB. (1983) Grass Systematics, Texas A&M Univ. Press, College Station, 1-397.

Hayward DM, Parry DW. (1973) Electron-probe microanalysis studies of silica distribution in barley (Hordeum sativum L.), Ann. Bot. 37, 579-591.

Hodson MJ, Sangster AG, Parry DW. (1984) An ultrastructural study on the development of silicified tissues in the lemma of Phalaris canariensis L., Proc. Royal Soc. London, Series B, 222, 413-425.

Hodson MJ, Sangster AG, Parry DW. (1985) An ultrastructural study on the developmental phases and silicification of the glumes of Phalaris canariensis L., Ann. Bot. 55, 649-665.

Holmgren P, Keuken W, Schofield EK. (1981) Index Herbariorum, Part I. Guide to the Herbaria of the World, 7th ed. W. Junk, The Hague, Netherlands, 355-417.

Kaufman PB, Bigelow WC, Petering LB, Drogosz FB. (1969) Silica in developing epidermal cells of Avena internodes: electron microprobe analysis, Science, 166, 1015-1017.

Kaufman PB, Dayanandan Y, Takeoka Y, Bigelow WC, Jones JD, Iler R. (1981) Silica in shoots of higher plants, in Silicon and Siliceous Structures in Biological Systems, T.L. Simpson and B.E. Volcani (eds.), Springer-Verlag, NY, 409-449.

Kaufman PB, Dayanandan P, Franklin CI, Takeoka Y. (1985) Structure and function of silica bodies in the epidermal system of grass shoots, Ann. Bot. 55, 487-507.

Kaufman PB, Petering LB, Smith JG. (1970) Ultrastructural development of cork-silica cell pairs in Avena internodal epidermis, Bot. Gaz. 131, 173-185.

Lanning FC, Hopkins TL, Loera JC. (1980) Silica and ash content and depositional patterns in tissues of mature Zea mays L. plants, Ann. Bot. 45, 549-554.

Lau EM, Goldoftas M, Baldwin VD, Dayanandan P, Srinivasan J, Kaufman PB. (1978) Structure and localization of silica in the leaf and internodal epidermal system of the marsh grass Phragmites australis, Can. J. Bot. 56, 1696-1701.

Lawton JR. (1980) Observations on the structure of epidermal cells, particularly the cork and silica cells, from the flowering stem internode of Lolium temulentum L. (Gramineae), Bot. J. Linn. Soc. 80, 161-177.

Lewin J, Reimann BEF. (1969) Silicon and plant growth, Ann. Rev. Plant Physiol., 20, 289-304.

Metcalfe CR. (1960) Anatomy of the Monocotyledons. I. Gramineae, Oxford University Press, London, 1-731.

Newbury DE. (1977) Fundamentals of scanning electron microscopy for physicist: contrast mechanisms, Scanning Electron Miscrosc. 1977; I:553-568.

Palmer PG, Tucker AE. (1981) A scanning electron microscope survey of the epidermis of East African Grasses, I, Smithsonian Contr. Bot. 49, 1-84.

Palmer PG, Tucker AE. (1983) A scanning electron microscope survey of the epidermis of East African Grasses, II, Smithsonian Contr. Bot. 53, 1-72.

Parry DW, Hodson MJ. (1982) Silica distribution in the caryopsis and inflorescence bracts of foxtail millet (Setaria italica (L.) Beauv.) and its possible significance in carcinogenesis, Ann. Bot. 49, 531-540.

Parry DW, Kelso M. (1975) The distribution of silicon deposits in the roots of Molinia caerulea (L.) Moench and Sorghum bicolor (L.) Moench, Ann. Bot. 39, 995-1001.

Parry DW, Smithson F. (1958) Techniques for studying opaline silica in grass leaves, Ann. Bot. 22, 543-549.

Parry DW, Smithson F. (1964) Types of opaline silica depositions in the leaves of British grasses, Ann. Bot. 28, 169-185.

Pearsall DM, Trimble MK. (1984) Identifying past agricultural activity through soil phytolith analysis: a case study from the Hawaiian Islands, J. Archaeological Sci. 11, 119-133.

Price CW, Johnson DW. (1971) The use of backscattered-electron images in metallographic analyses of carbides, Scanning Electron Microsc. 1971: 145-152.

Robinson VNE. (1975) Backscattered electron imaging, Scanning Electron Microsc. 1975: 51-60.

Salisbury FB, Ross CW. (1978) Plant Physiology, Wadsworth, Belmont, CA, 83.

Sangster AG. (1970) Intracellular silica deposition in immature leaves in three species of the Gramineae, Ann. Bot. 34, 245-257.

Sangster AG. (1977) Electron-probe microassay studies of silicon deposits in the roots of two species of Andropogon, Can. J. Bot. 55, 880-887.

Sangster AG. (1985) Silicon distribution and anatomy of the grass rhizome, with special reference to Miscanthus sacchariflorus (Maxim.) Hackel, Ann. Bot. 55, 621-634.

Sangster AG, Hodson MJ, Parry DW. (1983a) Silicon deposition and anatomical studies in the inflorescence bracts of four *Phalaris* species with their possible relevance to carcinogenesis, New Phytol. **93**, 105-122.

Sangster AG, Hodson MJ, Parry DW, Rees JA. (1983b) A developmental study of silicification in the trichomes and associated epidermal structures of the inflorescence bracts of the grass *Phalaris canariensis* L., Ann. Bot. **52**, 171-187.

Sangster AG, Parry DW. (1981) Ultrastructure of silica deposits in higher plants, in Silicon and Siliceous Structures in Biological Systems, T.L. Simpson and B.E. Volcani (eds.), Springer-Verlag, NY, 383-407.

Shaw RB, Smeins FE. (1981) Some anatomical and morphological characteristics of the North American species of *Eriochloa* (Poaceae: Paniceae), Bot. Gaz. **142**, 534-544.

Takeoka Y, Matsumura O, Kaufman PB. (1983) Studies on silicification of epidermal tissues of grasses as investigated by soft x-ray image analysis I. On the method to detect and calculate frequency of silica bodies in bulliform cells, Japan. J. Crop Sci. **52**, 544-550.

Takeoka Y, Wada T, Naito K, Kaufman PB. (1984) Studies on silicification of epidermal tissues of grasses as investigated by soft x-ray image analysis II. Differences in frequency of silica bodies in bulliform cells at different positions in the leaves of rice plants, Japan. J. Crop Sci. 53, 197-203.

Terrell EE, Wergin WP. (1979) Scanning electron microscopy and energy dispersive x-ray analysis of leaf epidermis in *Zizania* (Gramineae), Scanning Electron Microsc. 1979; III:81-88.

Terrell EE, Wergin WP. (1981) Epidermal features and silica deposition in lemmas and awns of *Zizania* (Gramineae), Amer. J. Bot. 68, 697-707.

Terrell EE, Wergin WP, Renvoize SA. (1983) Epidermal features of spikelets in *Leersia* (Poaceae), Bull. Torrey Bot. Club, 110, 423-434.

Twiss PC, Suess E, Smith RM. (1969) Morphological classification of grass phytoliths, Soil Sci. Soc. Amer. Proc. 33, 109-115.

Watson L, Dallwitz MJ. (1980) Australian Grass Genera. Anatomy, Morphology, and Keys, Australian National University, Canberra, 1-209.

Wells OC. (1977) Backscattered electron image (BEI) in the scanning electron microscope (SEM), Scanning Electron Microsc. 1977; I:747-771.

Table 1. Predominant types of silica bodies found in subfamilies of North American grasses (Metcalfe, 1960; Clifford and Watson, 1977; Gould and Shaw, 1983).

Subfamily*	Silica Body Type
POOIDEAE	horizontally elongated tall and narrow crescent
PANICOIDEAE	cross dumbbell
CHLORIDOIDEAE	saddle
BAMBUSOIDEAE	cross dumbbell saddle olyroid
ORYZOIDEAE	oryzoid
ARUNDINOIDEAE	no predominant type

*Classification according to Gould and Shaw, 1983

Figure 1. Line scan of silicon x-ray window in leaf of rice (*Oryza sativa*). Image electronically shifted 90° from original. Lower arrowheads: location of scan through two epidermal papillae (left), basal portion of one silica body (center), then grazing two more epidermal papillae (right). Upper arrowheads: relative intensity of Si signal in corresponding region traversed by line scan.

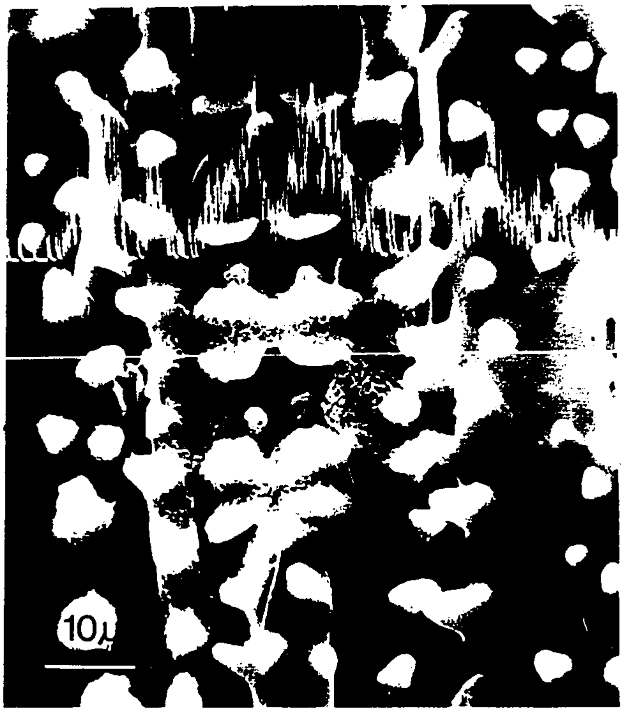
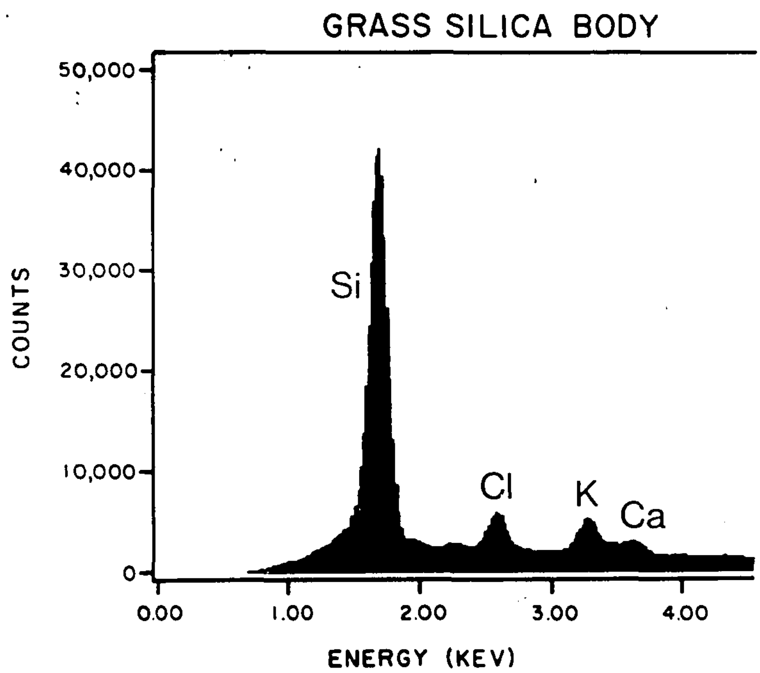

10μ

Figure 2. X-ray energy spectrum of silica body, *in situ*, displaying a high count rate for energy values diagnostic of silicon.



GRASS SILICA BODY
50,000
40,000
30,000
20,000
10,000
0
COUNTS
Si
Cl
K
Ca
0.00
1.00
2.00
3.00
4.00
ENERGY (KEV)

Figure 3. Subsurface silica bodies in leaf of little bluestem (*Schizachyrium scoparium*: Panicoideae). Longitudinal axis of leaf viewed vertically. a) secondary electron image; b) matched elemental area map for Si; c) matched backscattered electron image.

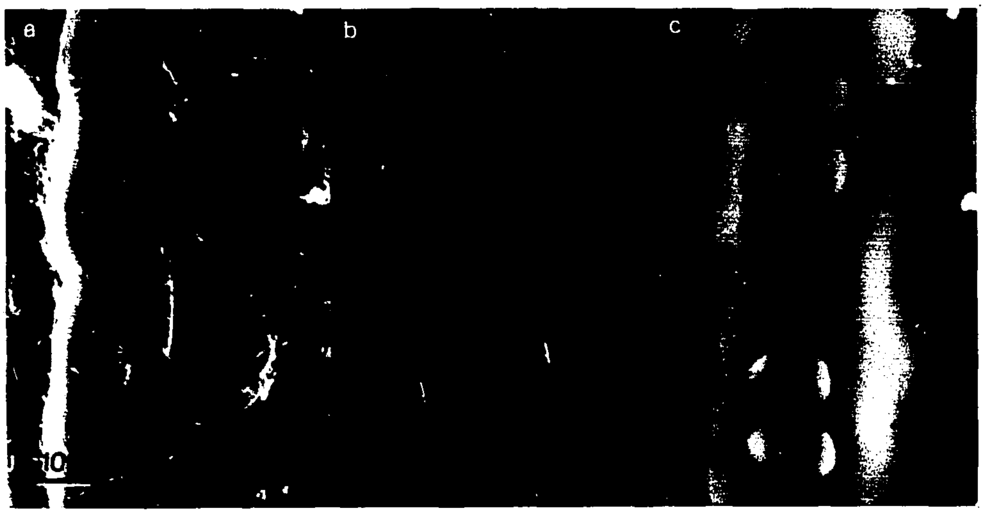
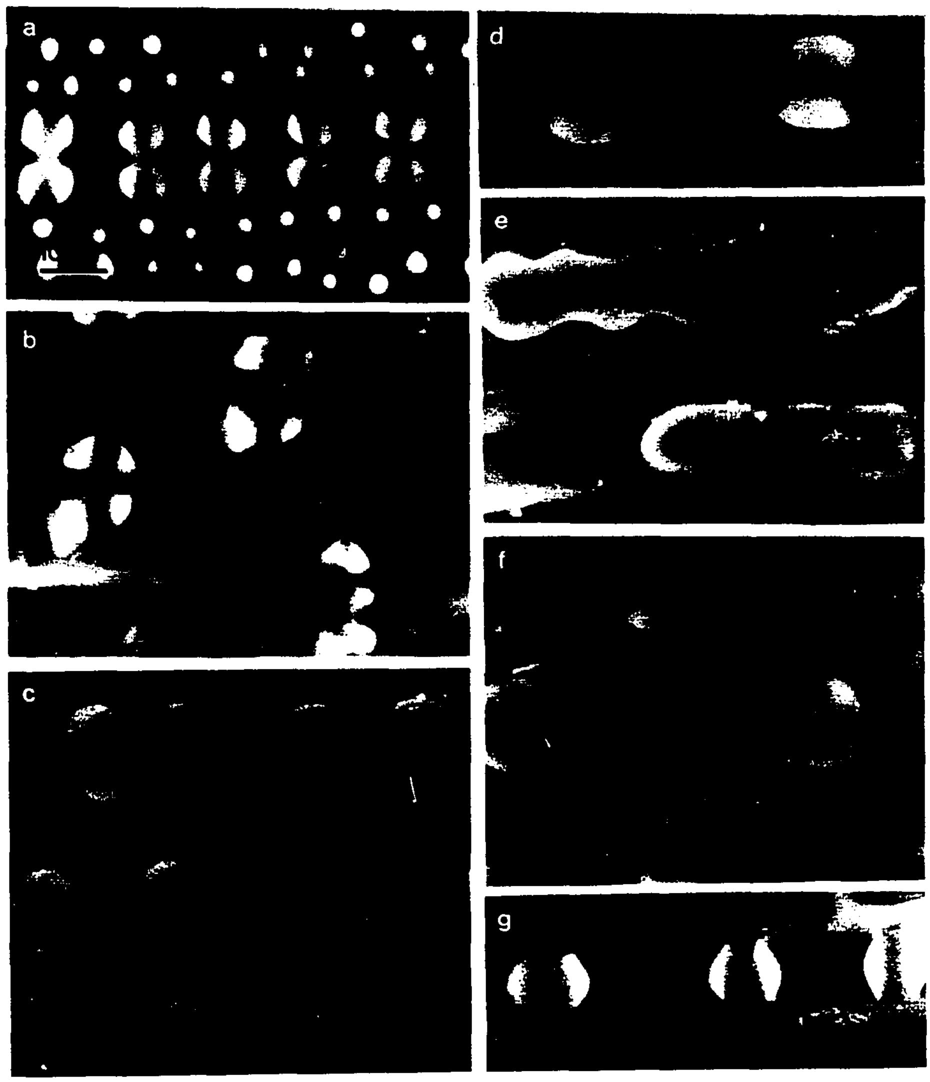

a
b
c
10

Figure 4. Types of silica bodies in grasses representative of subfamilies of North American Poaceae. a) oryzoid (center row): rice (*Oryza sativa*: Oryzoideae); b) olyroid (lower right-hand corner) and cross-shaped: (*Pariana* sp.: Bambusoideae); c) cross-shaped (lowermost) and dumbbell-shaped: Johnson grass (*Sorghum halepense*: Panicoideae); d) saddle-shaped: hairy grama (*Bouteloua hirsuta*: Chloridoideae); e) horizontally elongated: oats (*Avena sativa*: Pooideae); f) circular-shaped (center row, left and right) and saddle-shaped (upper and lower): common reed (*Phragmites australis*: Arundinoideae); g) acutely angled: (*Isachne pallens*: Panicoideae)--example of BEI with metal-coated specimen.


a
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CHAPTER 4

Descriptions for Poaceae: _Vascular Flora of the Southeastern United States_.

Preface

The descriptions in this chapter are contributions to the volume treating the Poaceae for the Vascular Flora of the Southeastern United States, to be published by the University of North Carolina Press, Chapel Hill. These accounts have been written in the format for the Poaceae that I drew up jointly with James Estes. In addition, they follow the guidelines set forth in the Contributor's Guide for the Flora, written by J.R. Massey and the Editorial Board.

The descriptions of the included taxa are based on loans from the following herbaria: AUA, CLEMS, DHL, DOV, DUKE, FLAS, FSU, KY, LSUM, LYN, MARY, MEM, MISS, MUR, NCSC, NCU, NLU, SMU, TAES, TENN, UARK, UNA, USF, VPI, and WVA.

AMMOPHILA

Ammophila breviligulata Fern. Rhizomatous perennial; rhizomes deep, stout, and scaly, 4-5 mm in diam. Culms erect, unbranched, 5.2-13 dm tall, nodes and internodes glabrous; sterile and fertile culms intermixed; leaves cauline, mostly crowded toward lower part of culm. Sheaths open, rounded, longer than internodes, glabrous; strongly overlapping below; margins entire, scarious; lowermost, buried sheaths becoming fibrillose; sheath auricles present as rounded area continuous with sheath margins and ligule, as long as ligule, occasionally absent; margin ciliolate or entire. Ligules scarious, stiff, (0.5)1.2-3(4.6) mm long, glabrous; apex truncate or rounded, ciliolate; Collars yellowish, purplish, or indistinct, glabrous. Blades thick, linear, mostly involute and flattened at base, occasionally ± flat throughout, 15-80 cm long, 1.2-6.5 mm wide (unrolled) (0.5-2.5 mm rolled), lacking midrib; upper surface canaliculate, scaberulous, lower surface glabrous; apex long-attenuate, acute; margins entire or with widely spaced minute hairs. Inflorescence a contracted, cylindric spike-like panicle with strongly ascending and overlapping branches; stramineous, 13-40 cm long, 1-2(2.5) cm broad. Spikelets strongly laterally compressed, (8.5)10-15(18.5) mm long, floret one, disarticulating above the glumes; rachilla prolonged beyond palea as a short bristle to 2.8 mm long, with hairs to 1.9 mm long, rarely ± glabrous.

Glumes ± equal, papery, as long as spikelet, linear-lanceolate; apex acute; margins scarious, entire or occasionally with minute hairs; surface puberulent or scaberulous; first glume (7)10-15(18) mm long; nerve 1; second glume (8.5)11-15(18.5) mm long; nerves 3, lateral nerves sometimes faint. Lemmas awnless (rarely with subterminal mucro to 0.2 mm), lanceolate-linear, keeled but slightly rounded below, (8)10-12(14) mm long, papery, puberulent or smooth; nerves 5, weakly convergent, often faint, scaberulous; apex acute or blunt; margins scarious, entire or with minute hairs; callus oblique, with a tuft of hairs to 2-3(4.2) mm long. Paleas similar to lemmas, 6-10 mm long; nerves 2, scaberulous. Stamens 3, anthers linear, (4)5-6.2 mm long. Caryopses light orangish-brown, narrowly obovoid and ± circular in cross-section, 3-3.3 mm long, 1.0-1.5 mm broad, with minute beak. (n=14) Summer to late fall. Sandy areas, primarily beaches and dunes; an excellent sand-binder; AC. Del, Md, NC, and Va. (Ill, Ind, Ohio, Pa, NJ).

ARRHENATHERUM

Arrhenatherum elatius (L.) Beauv. ex J. & C. Presl. Cespitose-rhizomatous perennial; rhizomes short, to 3 mm in diam. Culms erect, unbranched, (4.6)6.7-16 dm tall, nodes glabrous or occasionally shortly pubescent; internodes hollow, glabrous or shortly pubescent immediately above and below nodes; leaves cauline and basal. Sheaths open, lower ± keeled, upper not keeled, mostly shorter than internodes, glabrous; margins scarious. Ligules scarious, 1-3 mm long, glabrous or scaberulous; apex rounded to ± truncate, erose and ciliolate, rarely entire. Collars narrow, yellowish. Blades linear, flat, 5-32 cm long, 2-10 mm wide; midrib generally only visible along lower portions of blade; upper surface scaberulous or sometimes shortly pilose, lower surface scaberulous, rarely shortly pilose; apices long acuminate, becoming involute upon drying; margins scaberulous; base noticeably flared and yellowish-cartilaginous thickened. Inflorescence an open but ± congested panicle, generally ± narrow but spreading in anthesis, (4.5)7-27(36) cm long, 1-6(10) cm broad, green, ± shining, becoming stramineous with age, occasionally slightly purple tinged; branches loosely-ascending, verticillate or fascicled at nodes, nodes ± widely spaced but internodes normally obscured by ascending branches, branches (except lowermost) about as long as internodes; axes, branches and pedicels all scaberulous; branches generally flowered to base; branches and pedicels often flexuous; Spikelets laterally compressed, 7.5-11 mm long; florets 2, disarticulating above the glumes, the two florets falling together, rarely disarticulating above glumes and between florets; pale or green, sometimes purple tinged; rachilla prolonged behind upper floret as a slender, delicate bristle, dorsally flattened and wider below, 1.2-2 mm long, often with a small club-shaped rudiment at apex. Glumes two, pale, thin, scarious (sometimes purple tinged), entirely scaberulous or occasionally internerves glabrous; first glume lanceolate or elliptic, 1/2-3/4 as long as lower lemma, 4-7.5 mm long, 1-nerved, apex acute; margins entire or scaberulous above middle; second glume broadly lanceolate to elliptic, longer and broader than first glume, second glume 3/4 to as long as second lemma; 6-11 mm long; nerves 3, parallel. Lemmas awned or awnless, acute, much firmer than glumes, 7-10 mm long, nerves (5)7, weakly convergent; scaberulous (or rarely glabrous) and generally sparsely hirsute; apices acute, hyaline; margins hyaline, scaberulous; callus bearded with hairs to 3.7 mm long; rachilla internode between florets subsessile or to 0.65 mm and stout. Lower floret staminate; lemma awned from below middle; awn stout, geniculate, very rarely ± straight, upwardly scaberulous, twisted below bend and usually with alternating light and dark bands, 10-20 mm long; paleas acute, scarious, 2-nerved, the nerves widely separated, ciliolate along nerves; shorter than lemmas, (5.2)6-8 mm long; upper floret perfect; lemma usually more hirsute than lower lemma, awned from below apex; awn straight, slender, scaberulous, 0.5-5 mm long, less commonly with an awn similar to awn of lower lemma but attached from the middle of lemma or above and to 15 mm long; rarely awnless; palea similar to that of lower floret, 6-8.5 mm long; Stamens 3, anthers linear, yellow-brown, (2.5)3.6-4.7(6) mm long. Caryopses linear-elliptic, pubescent, ± terete, pale golden-brown, 4-5 mm long, ca. 1.2 mm broad. (n=14) Late spring to early fall. Roadsides, fields, and meadows; all prov. SE except Del, Fla, and La. (Mo, Ill, Ind, Ohio, Pa, NJ). Native of Europe, naturalized in much of the US. *Arrhenatherum elatius* subsp. *bulbosum* (Willd.) Schubler & Martens has 1-6 cormlike, moniliform swollen internodes 3-13 mm in diam., and has been collected in Ala, Ark, Md, NC, Tenn, Va, and WVa.

BRACHYELYTRUM

Brachyelytrum erectum (Roth) Beauv. Cespitose perennial from short, knotty rhizomes; rhizomes 3-5 mm in diam. Culms erect, unbranched, 2.9-10.7 dm tall, solid; internodes glabrous or occasionally pubsecent; nodes moderately to densely retrorsely pubescent, rarely glabrous; leaves cauline. Sheaths open, rounded to ± keeled, generally shorter than internodes, glabrous or pubescent; margins scarious, entire or ciliate. Ligules scarious, 0.8-5 mm long, scaberulous or glabrous, occasionally with scattered hairs on surface; apex ± truncate, erose, coarsely toothed or ciliate. Collars densely pubsecent, rarely glabrous. Blades lanceolate to narrowly elliptic, flat, (3.4)9-16(23) cm long, (3)10-22 mm wide, midvein present; glabrous above or sometimes with hairs along main veins, pubescent along veins below, rarely glabrous; apex long acuminate; margins scaberulous and/or ciliate. Inflorescence a loose, few-flowered erect or nodding panicle 4.5-16 cm long, 0.75-2.0 cm broad, axes scaberulous or glabrous; spikelets ascending, attached obliquely to puberulent pedicels 0.5-13 mm long. Spikelets dorsally compressed, 8-13 mm long, with a single perfect floret, disarticulating above the glumes; rachilla prolonged, appressed to furrow of palea, scaberulous, 5-7 mm long. Glumes both present, or rarely first glume absent; first glume shorter than second glume, both considerably shorter than floret; _first glume_ generally a pale, small, thick triangular or subulate scale 1 mm or less in length, but occasionally to 3.6 mm; glabrous or puberulent; margins with scattered minute teeth; nerve 1 or not discernible; _second glume_ subulate or narrowly lanceolate, stiff, 0.5-5.5(7.9) mm long, glabrous, tapering to a fine tip or aristate, weakly laterally compressed, wider at the base which encircles base of rachilla, green with yellowish cartilaginous margins, nerve 1 or rarely 3 and weak; second glume separated from base of first glume by ca. 0.2 mm. _Lemmas_ awned, dorsally compressed, 7-12 mm long, chartaceous; nerves 5-9(10), convergent, hispid, scaberulous, or glabrous throughout or with trichomes only predominantly along nerves; margins enrolled around palea, entire, hyaline or sometimes thickened; callus beset with small hairs, abruptly rounded from rest of lemma, attached obliquely on a short thick stipe; apex tapering into a scaberulous, straight or wavy awn 11-28 mm long. _Paleas_ nearly as long as lemmas, glabrous, scaberulous or occasionally hispid along the 2 nerves; stiff but thinner than lemmas, pale green but hyaline along the margins, margins overlapping; apex with two slender teeth to 1.7 mm long, prominent narrow furrow along abaxial surface between the nerves. _Stamens_ 2, anthers yellow or yellowish-brown, (1.8)3-5.5(7.1) mm long. _Caryopses_ linear, minutely striate, reddish-brown with whitish scaberulous beak; (5.2)7-8.2 mm long including beak; beak 2-2.5 mm long, minutely 2-lobed at apex; shallowly furrowed along one side. (n=11) Summer to fall. Deciduous woods; all prov. SE (ALL). (ALL except Tex).

BRIZA

Briza minor L. Annual. Culms erect, unbranched, tillering at basal nodes, 0.8-7.0 dm tall, glabrous; internodes hollow, terete to ± flattened; leaves cauline and subbasal. Sheaths open, rounded, shorter than internodes, glabrous; margins broadly and conspicuously hyaline, entire; sheaths considerably longer on abaxial side. Ligules membranous, free portion attached much higher than where adaxial sheath margins join blade, glabrous, (0.8)1.5-4.5(5.5) mm long; apex rounded and entire, less commonly ± coarsely lacerate. Collars inconspicuous, glabrous. Blades flat, (2)4-20 cm long, 2-8 mm wide; midrib present but inconspicuous; upper surface glabrous or sparingly scaberulous, lower surface glabrous; apex acute; margins scaberulous; base outwardly folded, continuous well beyond free apical portion of ligule. Inflorescence an erect open panicle, (3)5-16 cm long, about as broad as long; branches capillary, scaberulous, 2 or 3 per node, spreading at maturity, several times rebranched; spikelets mostly solitary at tips of branchlets. Spikelets strongly laterally compressed, broadly triangular, (2)3-5(6) mm long; florets (3)4-7(11), crowded and overlapping, uppermost often staminate or neuter; disarticulation above the glumes and between the florets. Glumes 2, ± at right angles to rachilla axis; ± equal or second slightly longer, both somewhat longer than lemmas they subtend; broadly elliptic, rounded on back, papery, 1.5-2.7 mm long, glabrous; nerves 3 or 5, ± parallel; apex boat-shaped; margins entire, broad, scarious. Lemmas awnless, ± at right angles to rachilla axis; lower florets 1.3-2.5 mm long, upper progressively reduced, about as broad as long; central region of back rounded, saccate, thinly chartaceous, covered with minute elliptic scales (easily rubbed off). otherwise glabrous; nervation obscure; apex boat-shaped; margins scarious, broad, entire. Paleas ca. 1.3 mm long on lower forets, thinly chartaceous, glabrous inside, covered with scales on outside; nerves 2, broadly spaced, keels minutely winged below middle; apex acute; margins ciliate with scales. Stamens 3, anthers 0.75-1.3 mm long. Caryopses tightly invested by lemma and palea, ovoid to obovoid, ± flattened along one side, light brown, ca. 1.0 mm long, ca. 0.75 mm broad, smooth or scurfy. (n=5,7) Early spring to early summer. Roadsides, fields, woodlands, waste places; pied. and cp. SE except Ky, Md, and WVa. (NJ, Okla, Pa, and Tex). Native of Europe, naturalized in our area and Pacific coast.

CYNOSURUS

Annuals or perennials. Culms glabrous; internodes hollow, terete to ± flattened in cross-section. Sheaths open, rounded to slightly compressed; margins hyaline, entire. Ligules membranous, glabrous. Collars uneven, glabrous. Blades stiff-membranous; apex acute; margins entire or scaberulous; apex acute; margins entire or scaberulous; base ± flared and turned at junction with sheath. Inflorescence an erect, one-sided panicle; main branch giving rise to several "glomerules" of dimorphic spikelets; spikelets subsessile or on thick pedicels ca. 1.0-2.0 mm long, solitary or more often in pairs of 1 fertile-1 sterile. Spikelets dimorphic, the sterile distinctly unlike the fertile; sterile spikelets strongly laterally compressed, consisting of distichous slender empty lemmas and glumes; persistent on axis at maturity; sterile glumes and lemmas stiff, 1-nerved; fertile spikelets laterally compressed; glumes 2, subequal, 1-nerved, margins scaberulous; fertile lemmas stiff-membranous, laterally or dorsally compressed; nerves 5, convergent, often faint; ± glabrous on lower body of lemma, scabrous above; callus with small, ± swollen collar; paleas subequal to body of lemma, stiff-membranous, glabrous; nerves 2, each nerve ending in an apical tooth; margins entire; rachilla prolonged beyond uppermost floret as a minute or small, glabrous bristle; disarticulation above the glumes and between the florets. Stamens 3. Caryopses tightly enveloped by mature, ± indurate lemma and palea.

1. Panicles lanceolate to broadly oblong, bristly; fertile lemmas with awns 8.0-20 mm long ....*C. echinatus*

1. Panicles linear, narrow, not bristly; fertile lemmas with awn-tips 0.5-1.0 mm long ....*C. cristatus*

C. echinatus. Annual. Culms erect, unbranched or occasionally branching near base, 0.7-10.9 dm tall; leaves cauline. Sheaths shorter than internodes, glabrous or occasionally scaberulous. Ligules inserted at variable levels (see below), apical free portion 2.1-6.2 mm long; apex rounded to ± acute, entire or ciliolate. Collars somewhat flared at margins. Blades flat; midrib present but often inconspicuous; scabrous or rarely ± glabrous above and below; 4.2-21.5 cm long, 1.5-7.5 mm wide; margins of blades uniting with sheaths at variable levels, even on a single sheath. Inflorescence dense, bristly, lanceolate to broadly oblong in outline; 1.3-7.0 cm long, 1.0-3.0 cm broad; axes and pedicels glabrous or tuberculate. Sterile spikelets ovate to ± oval in outline, 7.0-15 mm long (including awns), 7.0-20 mm broad (including awns); sterile lemmas 8-15; glumes and sterile lemmas widely spaced and spreading to ascending below, becoming strongly overlapping and ascending above; rachilla thick, minutely tuberculate; sterile glumes subequal, setaceous, 7.0-13 mm long; body laterally compressed but not keeled, scaberulous or minutely tuberculate; margins scabrous; sterile lemmas awned, setaceous; scaberulous or minutely tuberculate; apex with straight or curved scabrous awn or with awn-tip; lower lemmas pale, 6.0-10 mm long (including awns), similar to glumes, body narrow and rounded on the back, margins scaberulous and very narrowly hyaline; upper lemmas green, 4.0-9.0 mm long (including awns), body broader and keeled, margins scaberulous and hyaline. Fertile spikelets elliptic in outline, 6.0-9.0 mm long (excluding awns); florets 2, the second rarely sterile or rudimentary, occasionally with a third (fertile or rudimentary) or fourth (rudimentary); glumes similar, longer than tip of body of uppermost floret, narrowly lanceolate, keeled to ± flat, 8.0-10 mm long, scarious, glabrous with scaberulous keel; apex with awn-tip 1.5-3.0 mm long; fertile lemmas awned, elliptic in outline, entire or scaberulous; awns scabrous, straight or gently curved, 8.0-20 mm long; body of first lemma 4.3-6.2 mm long, body of second lemma 4.1-5.3 mm long; rachilla joint between florets scaberulous, 0.75-1.3 mm long; prolonged rachilla slender, 0.6-1.1 mm long. paleas with apical teeth ca. 1.0 mm long, keels sometimes ciliolate. Anthers 1.4-2.3 mm long.

Caryopses narrowly ellipsoid, beaked by persistent style bases, light orange brown, smooth, 2.9-3.6 mm long, 1.0-1.2 mm broad. (n=7) Late spring to summer. Roadsides, fields, lawns, and waste places; mostly pied. and cp. SE except Del, Fla, Ga, Ky, and Tenn. (Mo, Ohio, Okla, and Pa). Native of Europe, sporadically introduced into the US.

C. cristatus. Cespitose perennial. Culms erect or ascending, unbranched, 2.7-5.8 dm tall; leaves cauline and low cauline. Sheaths shorter or longer than internodes, glabrous. Ligules sometimes longer on one side (when blade-sheath junction occurs at different levels on same blade), 0.4-1.9 mm long; apex ± truncate, coarsely erose. Collars yellowish or inconspicuous. Blades mostly flat, occasionally folded; midrib present, inconspicuous on upper surface; glabrous or minutely pubescent above, glabrous below; upper cauline blades 6.0-17.5 cm long, lower cauline blades 6.5-27 cm long; all blades 1.0-3.0(5.0) mm wide. Inflorescence narrow, linear in outline, straight or curved; 2.0-10.5 cm long, 4.0-10(13) mm broad; axes and pedicels shortly pubescent. Sterile spikelets obovate to obdeltoid in outline, 3.0-5.4 mm long, (1.7)2.5-3.5(4.5) mm broad; sterile lemmas 4-10; glumes and sterile lemmas ascending, lowermost lemmas closely spaced but not or little overlapping, uppermost strongly overlapping;

rachilla thick, minutely pubescent and minutely tuberculate; sterile glumes similar to sterile lemmas, (2.0)2.5-4.7 mm long; sterile lemmas linear-lanceolate, strongly keeled, glabrous, apex sharply acuminate; margins hyaline, entire; lower lemmas 2.6-4.2 mm long, upper lemmas 1.3-2.8 mm long. Fertile spikelets broadly elliptic to obovate in outline, 3.0-5.4 mm long; florets 2-5, uppermost may be sterile or rudimentary; glumes similar, 2/3 as long to just longer than tip of uppermost lemma, linear-lanceolate, strongly keeled, (2.5)3.3-4.4(5.2) mm long, stiff, glabrous or scaberulous, with scabrous keel; apex acuminate to sharp point or awn-tip; fertile lemmas lanceolate in outline, entire or scaberulous; apex with awn-tip ca. 0.5-1.0 mm long; first lemma 2.6-4.0 mm long, second lemma 2.3-3.6 mm long, third lemma 2.2-3.1 mm long (all excluding awn-tips); paleas with minute apical teeth, keels entire or scaberulous near apex. Anthers 1.3-2.0 mm long. Caryopses lanceolate, dark brown, ca. 2.5 mm long, ca. 0.5 mm broad, virtually inseparable from mature lemma and palea. (n=7) Summer. Waste places and lawns; mts. and pied. Md, NC, and WVa. (Ind, NJ, Ohio, and Pa). Native of Europe, sporadically introduced into the US.

DACTYLOCTENIUM

Annuals (ours). Culms decumbent or ascending, sometimes erect; prostrate culms rooting at lowermost nodes and plants then mat-forming. Erect portion of culms branched or unbranched; nodes and internodes glabrous; internodes sponge-filled and soft, sometimes flattened; leaves cauline. Sheaths open, keeled or rounded, usually shorter than internodes, glabrous; apex papillose-ciliate or glabrous; margins scarious, entire. Ligules membranous at base; apex ± truncate, ciliolate. Collars glabrous or occasionally pubescent. Blades green, linear to linear-lanceolate, flat or folded; midrib present; upper and lower surfaces glabrous or pubescent; margins entire, scaberulous or ciliate; apex acute. Inflorescence consisting of many-flowered one-sided spikes, these digitately arranged at apex of culm; spikes ascending or horizontal; tuft of hairs at apex of culm; rachis triangular, normally scaberulous along margins, otherwise glabrous; apex extending beyond point of spikelet attachment; spikes deciduous or persistent. Spikelets sessile, chartaceous, imbricate and alternating in 2 rows along lower side of rachis, progressively reduced toward apex of spike, the distal-most rudimentary; spikelets strongly laterally compressed, several-flowered, generally only uppermost reduced and sterile; spikelets disarticulating or persisting. Glumes subequal; nerve 1, glabrous; margins hyaline; keeled, scaberulous along keel; awned or awnless. Lemmas awnless, glabrous, scaberulous-keeled; nerves 3, parallel or weakly-converging, the lateral near the outer margin and frequently faint; apex acuminate, with slender tip and this often recurved; margins hyaline. Paleas glabrous; nerves 2, scaberulous, deeply concave between nerves; wingless or rarely winged; apex acute or broadly acuminate; margins scarious. Stamens 3. Caryopses modified; seed initially free and invested in a thin pericarp, this splitting and withering at maturity; seed (ours) orange-brown, subglobose-broadly obovate, beset with prominent transverse ridges; entire plant or any part thereof may be tinged with purple.

1. Individual spikes (0.7)1.5-7.5 cm long, arranged loosely at culm end; larger spikelets 3-4.7 mm long; acuminate apex of lemma tapering from upper 1/3 or 1/4 of body ....*D. aegyptium*

1. Individual spikes 0.5-1.2 cm long, arranged in a compact, ± globose cluster at culm end; larger spikelets 4.6-6.6 mm long; acuminate apex of lemma tapering from the middle of the body ....*D. radulans*

D. aegyptium (L.) Willd. Culms with erect portion unbranched or branched from lower half, 0.4-7.7 dm tall. Sheaths keeled or rounded, upper margin papillose-ciliate, occasionally entire. Ligules 0.4-1.4(2.4) mm long. Collars normally glabrous, occasionally puberulent or with a ring of short hairs to 0.6 mm. Blades flat or folded, 1-35 cm long, 1-9 mm wide; upper and lower surfaces sparsely papillose-hispid, especially toward apices, rarely glabrous; margin scaberulous, papillose-ciliate on lower 3/4, rarely eciliate. Inflorescence with (1)2-7(11) spikes; spikes ascending or horizontally spreading, (0.7)1.5-7.5 cm long; rachis apex extending (1)2-4 mm beyond point of spikelet attachment; rachis often with tuft of hairs subtending each spikelet; spikes generally persisitent on axis. Spikelets broadly elliptic-ovate to ovate, lead-green or stramineous, 3-4.7 mm long; florets 3-4(6); disarticulation above first glume, florets deciduous from rachilla or not. Glumes 1.4-2.5(3) mm long; first glume lanceolate-elliptic ovate, awnless, apex acute; second glume narrowly obovate or elliptic ovate, with midnerve extending into a scaberulous stout flexous (occasionally straight) awn 1.2-2.5 mm long; occasionally apex only apiculate. Lemmas (fertile) ovate to ovate-elliptic 2.4-3.75 mm long. Paleas narrowly ovate, 1.6-2.75 mm long, rarely with wing along keel and this extending nearly to apex. Anthers 0.2-0.9 mm long. Seeds 0.68-1mm long, 0.64-1.1 mm broad. (n=10, 18, 20, 24) Early summer to early winter. Disturbed habitats; cp. Ala, Ark, Fla, Ga, La, Miss, NC, and SC. (Tex, Ill, Penn, and NJ). Native of Old World Tropics, naturalized in our area and a few other states.

D. radulans (R. Br.) Beauv. Culms with erect portion freely branching, less commonly unbranched, 0.85-3.6(5.5) dm tall. Sheaths rounded or slightly keeled; apex occasionally with a few scattered hairs. Ligules 1-1.5 mm long. Collars glabrous. Blades flat, 10.5-19 cm long, 2-6 mm wide; upper and lower surfaces glabrous, scabrous, or with pustular-based hairs; margins ciliate with pustular-based hairs especially on lower 1/2, otherwise entire or scaberlous. Inflorescence with 5-10(15) spikes; spikes 0.5-1.2 cm long, arranged in a ± globose cluster, rarely with an additional solitary spike produced below (ca. 5 mm) the terminal cluster; rachis sometimes with a few short hairs at base of spikelet, rachis apex extending 0.65-1.8 mm beyond point of spikelet attachment; disarticulation at base of spikes, the individual spikes falling whole. Spikelets elliptic-obovate, green or stramineous, (3.2)4.6-6.6 mm long, florets (2)3-4(6); florets generally persistent on rachis. Glumes (1.7)2.5-3.3 mm long; first glume lanceolate, awnless, apex acute; second glume elliptic to narrowly obovate, with midnerve extending into a straight or curved awn (0.3)0.8-1.9 mm long, sometimes merely aristate. Lemmas (fertile) broadly ovate, 2.5-4.7 mm long. Paleas narrowly elliptic-ovate, 1.2-3.3 mm long. Stamens with anthers (0.45)0.5-0.6(1.8) mm long. Seeds 0.9-1.2 mm long, 0.6-0.9 mm broad. Late spring to summer. Native to Australia, and collected in the late 1950's-early 1960's around wool combing mills in Berkeley and Florence Counties, South Carolina.

DESCHAMPSIA

Cespitose perennials (ours). Culms erect, fertile culms unbranched; internodes hollow, terete or ± flattened in cross-section; leaves cauline and basal, the latter often numerous. Sheaths open; margins narrowly hyaline, entire. Ligules stiff membranes. Blades stiff, midrib not discernible. Inflorescence a panicle, branches and peduncles scabrous or scaberulous. Spikelets laterally compressed, ellipsoid(closed); florets 2(3), essentially alike, fertile; rachilla prolonged beyond uppermost floret as a hairy bristle; disarticulation above the glumes, the florets either remaining attached or falling separately. Glumes 2, awnless. Lemmas dorsally awned. Paleas 2-nerved, scaberulous along keels; margins entire. Stamens 3.

1. Panicle narrow, ca. 1.0 cm broad; branches appressed or less often loosely ascending; lemmas chartaceous ....*D. elongata*

1. Panicle broadly ovate to elliptic, 3.0-17 cm broad; branches ascending to spreading; lemmas scarious

    2. Awns of lemmas twisted, geniculate; prolonged rachilla less than 1/4 as long as its lemma; basal blades filiform and tightly involute ....*D. flexuosa*

2. Awns of lemmas straignt or somewhat bent but not decidedly geniculate; prolonged rachilla 1/3 as long to nearly as long as its lemma; basal blades mostly flat or a few involute ..*D. cespitosa*

D. elongata (Hook.) Munro ex Benth. *Culms* glabrous or scaberulous, 3.5-7.5 dm tall. *Sheaths* rounded to somewhat keeled, longer than internodes, glabrous. *Ligules* glabrous, 3.9-7.5 mm long; apex acute or acuminate. *Collars* yellowish, glabrous. *Blades* green, flat or involute, scabrous above and below; apex ± acute; margins scaberulous; culm blades 10-30 cm long, basal blades (4)10-30 cm long; involute baldes ca. 0.5 mm wide, flat blades 1.0-2.0 mm wide. *Inflorescence* a narrow but loose panicle, elongate, 11-31 cm long, ca. 1.0 cm broad; branches appressed or less often loosely ascending, ± straight, scabrous. *Spikelets* mostly green, sometimes tinged with bronze or purple, 3.3-5.0 mm long; rachilla joint between florets ca. 1.0 mm long, with hairs ca. 0.5 mm long. *Glumes* membranous, subequal, as long as spikelet, 3.3-5.0 mm long, narrowly lance-elliptic, scaberulous; nerves 3, convergent; apex acute or acuminate; margins hyaline, entire. *Lemmas* similar to each other, chartaceous, lance-ovate to elliptic, glabrous, shiny; nerves 4, obscure; apex prominently bifid, each tooth subdivided into one smaller (inner) and one larger (outer) tooth; margins entire; callus with a tuft of hairs ca. 1.0-1.5 mm long; first lemma 1.8-2.5 mm long; second lemma 1.5-2.1 mm long; prolonged rachilla from 1/3 as long to nearly as long as its lemma, with hairs ca. 0.5 mm long; awn from just below middle or base, slender, straight, normally exserted but sometimes included, 2.1-5.2 mm long. Paleas extending to base of lateral teeth of lemma, hyaline, glabrous; apex minutely bifid. Anthers ca. 0.5-0.6 mm long. Caryopses narrowly obovate, light orange brown, beaked by light yellow persistent style bases, minutely wrinkled, ca. 1.0-1.3 mm long, ca. 0.5 mm broad. (n=13) Late spring. Native to western North America, and collected once in 1960 around a wool combing mill in Berkeley County, South Carolina.

D. flexuosa (L.) Beauv. Culms glabrous, 2.5-8.3 dm tall. Sheaths rounded, shorter than internodes, glabrous or scaberulous. Ligules scaberulous, 1.3-3.0 mm long on culm leaves, 0.3-1.0 mm long on basal leaves; apex rounded, acute, or ± truncate; ciliolate, ± entire, or erose, often splitting longitudinally at maturity. Collars inconspicuous, glabrous or scaberulous. Blades green to green-stramineous, filiform and tightly involute, glabrous or scaberulous below, upper surface not visible; apex ± blunt; margins not visible; culm blades 3.0-15 cm long, basal blades 2.0-25 cm long; all blades ca. 0.5 mm wide. Inflorescence an open panicle, broadly ovate to elliptic in outline, (4.0)7.0-15 cm long, (2.0)4.0-10(15) cm broad; branches ascending to spreading, flexuous, capillary, spikelets mostly solitary at tips of branchlets. Spikelets green or bronze, often suffused with purple, 4.0-5.0(6.0) mm long; rachilla joint between florets ca. 0.5 mm long, with hairs ca. 0.5-1.0 mm long. Glumes scarious, glabrous to scaberulous, 1-nerved; apex ± acute; margins entire to scaberulous; first glume shorter than first lemma, narrowly lanceolate, 2.9-4.3 mm long; second glume longer than first glume, as long as or just shorter than spikelet, lance-elliptic, 3.3-5.1 mm long. Lemmas similar to each other, scarious, narrowly lance-oblong, glabrous to scaberulous, with central groove dorsally; nerves 4, weakly convergent; apex ± acute; margins entire to scaberulous; callus with a tuft of hairs 0.75-1.0 mm long; first lemma (3.0)3.5-4.4 mm long; second lemma ca. 0.5 mm shorter than first lemma; prolonged rachilla 0.15-0.8 mm long, with a few hairs near apex; awn from near base, slender, twisted, geniculate, conspicuously exserted from floret, (3.7)4.5-6.0 mm long. Paleas from just shorter than to just longer than lemmas, scarious, glabrous to scaberulous; apex acute to ± bifid. Anthers 1.8-2.7 mm long. Caryopses narrowly fusiform, flattened along one side, light brown, smooth or rugulose, 2.0-2.8 mm long, 0.5-0.7 mm broad. (n=14) Late spring to summer. Rocky woods, rock outcrops, and balds; mts. and pied. Ala, Ark, Del, Ga, Md, NC, SC, Tenn, Va, and WVa. (NJ, Ohio, Okla, and Penn).

D. cespitosa (L.) Beauv. Culms glabrous, 4.0-9.0 dm tall. Sheaths rounded, shorter than internodes, glabrous. Ligules glabrous, (2.0)3.0-5.9 mm long; apex rounded to acute. Collars inconspicuous, glabrous. Blades green, flat or involute, scabrous above, glabrous below; apex acute; margins scaberulous; culm blades 1.0-8.0 cm long, basal blades 4.0-32 cm long; involute blades 0.5-1.0 mm wide, flat blades 1.5-3.0(3.5) mm wide. Inflorescence an open panicle, broadly ovate to elliptic in outline, 13-29 cm long, 3.0-17 cm broad; branches ascending to spreading, flexuous, capillary, spikelets mostly solitary at tips of branchlets. Spikelets green of bronze, often suffused with purple, 2.7-5.2 mm long; rachilla joint between florets 0.75-1.6 mm long, with hairs ca. 0.5 mm long. Glumes scarious, mostly glabrous; apex acute; margins entire; first glume shorter than first lemma, narrowly lanceolate, (1.4)2.2-3.9 mm long, 1-nerved; second glume longer than first glume, extending about midway up second lemma, lance-elliptic, (2.0)2.7-4.3 mm long, (2)3-nerved, lateral nerves sometimes obscure above middle. Lemmas similar to each other, scarious, narrowly lanceolate, glabrous to scaberulous; nerves 4, ± parallel; apex with 2-4 jagged teeth; margins entire to scaberulous; callus with tuft of hairs 0.5-1.7 mm long; *first lemma* (2.0)2.5-3.0(3.7) mm long; *second lemma* shorter than or subequal to first lemma, (1.0)1.7-3.0 mm long; prolonged rachilla from 1/3 as long to nearly as long as its lemma, with hairs ca. 0.5 mm long; awn from near base, slender, straight or somewhat bent but not decidedly geniculate, partially exserted from floret, (0.3)1.3-4.0 mm long. *Paleas* equal to or just shorter than lemmas, scarious, glabrous to scaberulous; apex prominently bilobed, lobes ca. 0.5 mm long, rounded, ciliolate. *Anthers* 1.0-2.0 mm long. No mature grains seen. (n=12,13,14) Summer. Open woods; mts. NC and WVa. (Ill, Ind, Ohio, and Okla). Incl. *D. cespitosa* var. *glauca* (Hartman) Lindman f.--R; *D. cespitosa* var. *parviflora* (Thuill.) Coss. & Germ.--F.

HOLCUS

Holcus lanatus L. Cespitose perennial from short caudex; Culms erect or geniculate at base, unbranched, 2.3-12.3 dm tall, hollow, leaves cauline and basal, nodes velvety-pubescent, middle internodes velvety-pubescent, lower and uppermost internodes puberulent or glabrous, (sometimes velvety-pubescent). Sheaths open, rounded to weakly keeled, generally shorter than internodes, velvety-pubescent; margins scarious, ciliate or entire. Ligules pale, scarious, 1.5-3.7 mm long, conspicuously continuous with margins of sheath, adaxial surface glabrous, abaxial surface densely and finely pubescent and with scattered long hairs; apex ± truncate, coarsely toothed, teeth ciliate or ciliolate, rarely ± entire. Collars narrow, pale, velvety-pubescent. Blades linear or lanceolate, flat, (1)4-15.5(30) cm long, (2)4-13 mm wide, blade of uppermost leaf usually much reduced, lanceolate, basal leaves often narrow and ribbonlike, midrib present and generally visible only on lower surface below middle; upper and lower surfaces and margins velvety-pubescent; apex acute. Inflorescence a loosely contracted, densely-flowered panicle, branches whorled at nodes; whitish, often purple-tinged, 2.5-25 cm long, 1.3-7 cm broad, at anthesis branches spreading and inflorescence more open and to 12 cm broad; branchlets flowered to base, axes shortly villous.

Spikelets broadly elliptic, (2.5)3.2-5.2 mm long, laterally compressed, disarticulating below the glumes, florets 2 (rarely 3), concealed within the glumes, lower perfect and upper staminate; rachilla prolonged beyond second floret as a minute, appressed peglike projection to 0.25 mm. Glumes two, first glume slightly shorter than second, second glume as long as spikelet, thin, white with green nerves becoming stramineous with age, all nerves keeled, ciliate; margins entire or ciliolate; glumes softly puberulent or pubescent, or sometimes scaberulous, occasionally internerves ± glabrous; often purple tinged; first glume (2.4)3-5 mm long, nerve 1; apex acute or aristate; second glume broader than first glume, as long as spikelet; nerves 3; apex occasionally acute; normally aristate or with a subterminal awn, straight, slender, or slightly curved, to 1.3 mm. Lower floret perfect, raised on a curved stipe 0.3-0.7 mm long; lemma awnless, rounded on back, (1.4)1.9-2.5 mm, much thicker than glumes, pale green when young -- pale brown, smooth and shining when mature; nerves 5, obscure or faint, midnerve sometimes ciliolate; apex obtuse or subacute, ciliolate; callus with a few slender bristles to 1.5 mm; margin entire; palea hyaline, from just shorter than to longer than lemma, (1.4)1.7-2.5 mm long; nerves 2, gradually widening toward apex; glabrous or ciliolate; margins entire; broadly 3-lobed at apex, the lobes rounded, ciliolate, the middle lobe (between the nerves) longer than lateral lobes. Upper floret separated on rachilla (0.3).5-.6(.8) mm from lower floret, staminate, similar to lower floret but smaller (1.4-2.5 mm), with shorter callus hairs, and bearing from middle or above a short, stout curved or recurved (hooklike) yellowish awn 0.8-3 mm long, this included within glumes or tip sticking out of glumes. Lemmas 1.3-2.6 mm long; Palea 1/2 to as long as lemma. Stamens 3, anthers yellow or orangish, sometimes purple tinged, (1)1.8-2.7 mm long. Third floret rarely present, awned or awnless. Lodicules lanceolate, hyaline, 0.6-0.75 mm long, sometimes with lateral tooth. Caryopses yellowish, ellipsoid, smooth, 1.5-2.1 mm long, ca. 0.6-0.7 mm broad, palea adhering and leaving impression (shallow groove) in grain from middle and below. (n=7) Spring to early fall. Disturbed habitats; all prov. SE except Del and Fla. (Mo, Ill, Ind, Ohio, Pa, and NJ). Native of Europe, naturalized in much of the US.

MILIUM

M. effusum L. Cespitiose perennial from rhizomes 1-4 mm in diam. Culms erect, unbranched, 4.7-15.5 dm tall; internodes striate, hollow, easily compressed; nodes and internodes glabrous; leaves cauline. Sheaths open, not keeled, mostly shorter than internodes, glabrous, margins hyaline, entire. Ligules scarious, (2)5-8 mm long, rarely wanting, glabrous; apex erose or variously irregularly toothed or cleft. Collars yellowish. Blades linear, flat, 7.4-36 cm long, 4-17 mm wide; midrib present; glabrous above, glabrous or scaberulous below; margins scaberulous. Inflorescence an open panicle, 15-38 cm long, 6-15 cm broad, branches capillary, whorled, (1)2-4(5) per node, spreading or drooping, nodes widely spaced; primary branches sparsely rebranched, branchlets scaberulous and bearing spikelets on outer 1/2-1/3, or occasionally with spikelets to base; lower nodes of inflorescence with complete or partial ring (collar) of whitish cartilaginous tissue. Spikelets dorsally compressed, (2.4)3-3.3(3.9) mm long; floret 1, perfect, disarticulating above the glumes. Glumes subequal, as long as spikelet, green but becoming stramineous with age, elliptic, membrenaceous, scaberulous or occasionally glabrous; nerves 3, parallel; apices acute; margins and apices conspicuously white hyaline when young, scaberulous; margins of first glume slightly overlapping second glume. Lemmas awnless, elliptic, rounded on back, just shorter than glumes, (2.2)2.5-3 mm long, obscurely nerved or sometimes 5 faint nerves discernible; chartaceous and greenish when young, becoming indurate, smooth, and shiny, color changing to brownish or dull white; apex acute, rarely obtuse; margins narrowly hyaline, enclosing palea. Paleas slightly shorter than lemmas, of similar texture and color; nerves 2, sometimes faint; apex obtuse; margins hyaline, involute. Stamens 3, anthers dull yellow to yellowish-brown, 1.4-2 mm long, ca. 1.0-1.2 mm broad. Caryopses dark orange-brown or reddish brown, ellipsoid, 1.7-2(2.5) mm long, minutely striate and rugose in places. (n=14) Late spring to late summer. Deciduous woods; mts. Md, NC, Va, and WVa. (Ill, Ind, Ohio, Pa, and NJ).

SCLEROCHLOA

Sclerochloa dura (L.) Beauv. Annual. Plants often matted, occasionally solitary; green but becoming stramineous with age; Culms generally procumbent to ascending, sometimes erect; unbranched, 2.0-18(30) cm tall, though generally less than 15 cm tall; culms many from tillering at basal nodes; nodes glabrous; internodes glabrous, solid or hollow with narrow lumen, ± flattened; leaves basal and cauline, strongly overlapping toward base, usually overtopping inflorescences. Sheaths closed and tubular in lower 1/4 to 1/2, open above; ± rounded on lower leaves, rounded to keeled on upper leaves; longer than internodes, glabrous; margins conspicuously and broadly hyaline; upper sheaths often inflated; auricles absent. Ligules membranous, broadly triangular, (0.3)0.75-2.0(3.3) mm long, glabrous; margins entire to ± lacerate; apex acute. Collars pale-white to yellowish white, glabrous. Blades flat or folded, (0.15)0.5-5.0(7.0) cm long, 1.0-4.0 mm wide; junction of blade and sheath not well defined; midrib present; glabrous above and below or midvein scaberulous; apex boat-shaped; margins entire or scaberulous. Inflorescence oblong to broadly elliptic, often partially enclosed in the upper leaf sheath(s), 1.0-4.0 cm long, 0.5-2.0 cm broad; spikelets overlapping on short, thick pedicels (or nearly sessile), arranged along one side of a ± zig-zag rachis; middle (and sometimes lower) nodes bearing short branches with 2-5 spikelets, spikelets solitary at upper (and usually lower) nodes; rarely with all nodes bearing only single spikelets; no general mode of disarticulation occurs; disseminules may consist of one or more florets, one or more spikelets, irregular pieces of inflorescence, or ± intact inflorescences. Spikelets narrowly oblong, laterally compressed, (3.4)5.0-12 mm long, glabrous; florets (2)3or4(7), upper one or two sterile; first floret ± sessile, remaining florets on ca. 0.5 mm thick rachilla joints 1.0-3.5 mm long. Glumes weakly dorsally compressed, both shorter than first lemma, awnless, chartaceous, glabrous; apices blunt or emarginate; margins broadly hyaline; first glume lanceolate to narrowly oblong, 1.4-3.0(3.7) mm long, nerves (1)3(5); second glume oblong to elliptic, longer than first glume, 2.6-5.4(6.2) mm long, nerves (3,5)7(9). Lemmas awnless, oblong to narrowly lanceolate, laterally compressed, (3.4)4.5-5.8(7.0) mm long in first floret, (0.4)1.0-4.5(5.9) mm long in remaining florets, chartaceous-indurate; incompletely and irregularly (5)7-9 nerved, nerves parallel; glabrous or scaberulous on midnerve toward apex; apex obtuse; margins broadly hyaline. Paleas dorsally compressed, ca. 0.5-1.5 mm shorter than lemma to equalling lemma; nerves 2, stiff, keels slightly winged in upper 1/2; glabrous, scaberulous along upper 1/2 of keels; apex blunt to variously lobed or notched; margins entire. Stamens 3, anthers 0.8-1.3 mm long. Caryopses yellowish-brown, narrowly lanceolate in outline, 2.1-3.5 mm long, ca. 0.75 mm broad; weakly trigonous; beaked by remnants of persistent styles/stigmas; surface rugulose. Lodicules 2, broadly oblong to oval, 0.75-1.0 mm long, clawed at base; apex entire to somewhat lacerate; margins entire. (n=7) Early spring, persisting to late spring. Collected on recreational ground in DeKalb Co., Ga, in bermuda sod supposedly obtained in Fla, where presently unknown; also collected in Washington Co., Ark; spreading in Okla and Mo.

CHAPTER 5

CAREX for Aquatic and Wetland Plants of Kentucky

Preface

This chapter constitutes the treatment of *Carex* (Cyperaceae) in: Beal, E.O. and J.W. Thieret. *Aquatic and Wetland Plants of Kentucky*, to be published by the Kentucky Nature Preserves, Frankfort, Kentucky. Included are those wetland species documented as occurring in Kentucky, as well as several species known from surrounding states but as yet not collected from Kentucky. These taxa are herein treated somewhat differently: (a) in the key, species names that have been underlined represent those taxa for which I have seen herbarium material from Kentucky. Names that have not been underlined represent either literature reports or species I feel are likely to be found in Kentucky; (b) only those taxa for which there exist herbarium record(s) or reliable literature reports(s) are illustrated; (c) each dot on the map indicates that I have seen a herbarium specimen of that taxon from that county; each triangle records a reliable literature report for that county. The dots are based on observations of specimens from the following herbaria: APSC, CINC, DHL, EKY, GH, KNK, KY, MEM, MUHW, MUR, NY, SIU, TENN, US, and WVA. Ranges for states other than Kentucky were taken primarily from Gleason and Cronquist (1963).

CAREX (Cyperaceae)

sedge

Grasslike perennial herbs. Flowers imperfect, without perianth, each borne in the axil of a scale; arranged in spikelets (called "spikes" by many authors). Spikelets solitary or in loose to compact clusters, terminal or lateral on the culm and usually subtended by involucral leaves or bracts. Staminate and carpellate flowers in the same or different spikelets; if in the same spikelet, the staminate above and the carpellate below, or vice versa; bristles absent; carpellate flowers and the succeeding achenes each enclosed in a sac, the perigynium, through the apical orifice of which the stigmas protrude at flowering time; style 2- or 3-cleft, disarticulating or persistent. Achene 2- or 3-sided.

References: Braun 1967; Gleason & Cronquist 1963; Mackenzie 1931-1935; Steyermark 1963; Voss 1972;

The task of deciding which species of *Carex* to include in a book on aquatic and wetland plants has been difficult. This is because of the large size of the genus and the wide variety of habitats that many of the species can occupy. Some sedges appear restricted to wet environments, but many species normally found in mesic woodlands can often be collected in low or even swampy woods. Indeed certain species, such as C. *caroliniana*, may be found in situations ranging from dry fields to water-filled ditches. The selection of species here is based on personal observation and on habitat information from herbarium specimens collected in Kentucky. While judgmental in nature, I hope it is sufficiently complete to account for most *Carex* species likely to be encountered in wet soil in Kentucky. For all species treated herein, whether they occur primarily in wet areas or not, only the wetland (as well as the potential wetland) habitats are given.

Keys are not entirely satisfactory to persons unfamiliar with *Carex*, and reference to the illustrations should aid in identification of an unknown sedge. So as not to further complicate an already large key, certain dry-to-mesic woodland sedge-groups such as the Laxiflorae have been intentionally omitted even though *C. blanda* and *C. leptonervia* of this group can sometimes occur in wet soil. The user is cautioned that if one of the species listed herein is not clearly indicated, a more comprehensive manual should be consulted.

Carex is an undercollected genus in Kentucky, and future collecting will reveal a much wider distribution for many species in this treatment and will lead to the discovery of wetland species not presently known from the state.

Authorities for the species names below follow Voss (1972) except that, for names not appearing in Voss, I used Gleason & Cronquist (1963).

Tips on Using the Key

The key to species below is based freely on the data in Mackenzie (1931-1935) and Braun (1967). A few of the key leads used by these and other authors are difficult, but they conveniently subdivide the genus into manageable groups and so are maintained here. Because they may present problems to persons having little experience at identifying sedges, the following discussion is given to help clarify them.

At several places in the key it is necessary to determine the location of staminate flowers in species having both staminate and carpellate flowers in the same spikelet(s). Anthers are generally not present on mature specimens, and the location of the region of staminate flowers is indicated by the occurrence of several "empty" scales (i.e., scales not subtending perigynia) together at the base or the tip of the spikelet. More often than not these scales are not truly empty but rather contain persistent staminal filaments, which may protrude from the scales or remain concealed behind them.

In Group E below, the user is asked to choose between long- and short-bracted species. This may best be determined by following the peduncle of the lowest spikelet downward to where the subtending bract diverges from the culm or from the sheath (if present). The measurement of sheath length is taken from here (the apex of the sheath) to its lowest point, i.e., where it arises from the culm. This latter point is usually marked by a slight swelling that is typically lighter - often pale yellow or whitish - than the rest of the culm; furthermore the culm is often slightly narrower beneath this point.

Perhaps the most difficult task one is faced with in the key is deciding whether the style disarticulates from or is persistent on the mature achene. As a supplement to this particular key character, the following _generalities_ can be added:

Style disarticulating (_Group E_): Carpellate spikelets (or carpellate portion of spikelet(s)) 2-8 mm broad (to 10 mm in _C. joorii_ and _C. buxbaumii_; perigynia not markedly inflated, 2-6 mm long (to 10 mm in _C. debilis_), beaked or beakless.

Style persistent (_Groups F, G,_ and _H_): Carpellate spikelets (or carpellate portion of spikelets) 8-40 mm broad; perigynia markedly inflated (not inflated in _C. comosa_ or _C. lacustris_ var. _laxiflora_), 5-20 mm long (4-5 mm in _C. frankii_), always prominently beaked.

In summary, Groups F, G, and H have broad carpellate spikelets that contain long, inflated, and prominently beaked perigynia. Familiarity with the illustrations of the species in these groups will be helpful.

Reliable identification of species of *Carex* requires mature perigynia. As is true with keys in general, several of each measurement should be taken. "Length" of perigynia includes both body and beak unless otherwise stated. "Width" of carpellate spikelets includes beaks as well as bodies of perigynia.

KEY TO GROUPS

1. Stigmas 2; achene 2-sided 2

1. Stigmas 3; achene 3-sided 4

   2. Spikelets of 2 kinds, the lowermost normally distinctly unlike the uppermost, many times longer than broad ....Group A

   2. Spikelets all alike (or essentially so), usually not over 3-6 times as long as broad 3

3. Spikelets (at least the terminal) with staminate flowers at tip ....Group B

3. Spikelets (at least the terminal) with staminate flowers at base ....Group C

   4. Spikelet solitary, terminal, staminate above, usually less than 5 mm broad ....Group D

   4. Spikelets 2 or more or, if solitary, then staminate below and more than 5 mm broad 5

5. Style jointed near base, eventually disarticulating and leaving the mature achene beakless or apiculate ....Group E

5. Style not jointed near base, persistent
on mature achene 6

6. Body of perigynium broadest above the
middle, inflated, abruptly and
truncately contracted to a long
slender beak ....Group F

6. Body of perigynium broadest at or
(more commonly) below the middle,
inflated or not, gradually tapering
or rounded at the summit, not
truncately contracted 7

7. Perigynia 5-10 mm long, inflated or not ....Group G

7. Perigynia 10-20 mm long, inflated ....Group H

GROUP A

1. Carpellate scales long-awned; carpellate
spikelets mostly all peduncled 2

1. Carpellate scales obtuse to acuminate;
carpellate spikelets (at least the upper)
sessile 3

2. Leaf-sheaths smooth; perigynia inflated, nearly round in cross-section; lower carpellate scales shallowly lobed at summit (on each side of awn) ....12. *C. crinita*

2. Leaf-sheaths hispidulous; perigynia more or less flattened; lower carpellate scales truncate or tapered at summit ....26. *C. gynandra*

3. Mature perigynia with a distinct, bent or twisted beak; lower carpellate spikelets mostly curved or drooping ....48. *C. torta*

3. Mature perigynia beakless or with a very short, straight beak; lower carpellate spikelets mostly erect ......47. *C. stricta* var. *stricta*

GROUP B

1. Inflorescence unbranched (the spikelets single at each node) 2

1. Inflorescence branched (at least at the lowermost node(s) with a branch bearing 2 or more spikelets) 3

2. Spikelets more or less globose (best seen on lower part of inflorescence); pergynia 3.6-4 mm long ....44. _C_. _socialis_

2. Spikelets narrowly oblong; perigynia (4)4.5-5.5 mm long ....6. _C_. _bromoides_

3. Leaf-sheaths tight; culms not flattened in drying; perigynia 2-3.5 mm long 4

3. Leaf-sheaths loose; culms flattened in drying; perigynia 3.5-9 mm long 6

4. Carpellate scales awned; leaf-sheaths usually cross-wrinkled on side opposite the blade ....52. _C_. _vulpinoidea_

4. Carpellate scales acute to mucronate (rarely a few lower scales with awns); leaf-sheaths not cross-wrinkled 5

5. Perigynia broadest above the middle, abruptly contracted into a beak ca. 0.5-1 mm long; principal leaves 5-8 mm wide ....17. _C_. _decomposita_

5. Perigynia broadest below the middle, tapering into a beak 1 mm or more long; principal leaves 1-3 mm wide ....39. C. prairea

6. Perigynia abruptly enlarged below into a disclike base ....14. *C. crus-corvi*

6. Perigynia corky below but not with a distinct disclike base 7

7. Perigynia ovate, the beak half as long to nearly as long as the body ....10. *C. conjuncta*

7. Perigynia lanceolate, the beak equal to or longer than the body 8

8. Leaf-sheaths cross-wrinkled on the side opposite the blade, not thickened at apex ....46. *C. stipata*

8. Leaf-sheaths not cross-wrinkled, cartilaginous-thickened at apex ....31. *C. laevivaginata*

GROUP C

1. Perigynia without winged margins (although often thin-edged), corky or spongy-thickened at base 2

1. Perigynia with winged margins, not corky or spongy-thickened at base. (Sedges

keying here belong to a difficult taxonomic complex, the Ovales. Botanists have split the group into many "species" on the basis of subtle morphological differences. Use of a more comprehensive manual - such as Gleason & Cronquist (1963) - is strongly recommended, as several members of this group not included in the key below could possibly be found growing in wet situations in Kentucky.) 3

2. Perigynia lanceolate, (4)4.5-5.5 mm long; spikelets narrowly oblong .....6. _C. bromoides_

2. Perigynia broadly ovate, 2.3-3.8 mm long; spikelets more or less globose ....4. _C. atlantica_ ssp. _atlantica_

3. Spikelets 1.5-3 cm long; perigynia 7-10 mm long ....37. _C. muskingumensis_

3. Spikelets normally less than 1.5 cm long; perigynia 3-6.5 mm long 4

4. Perigynia lanceolate, 3-5 times as long as broad 5

4. Perigynia narrowly ovate to suborbicular, not over 3 times as long as broad 6

5. Principal leaves 1-3 mm wide; leaf-sheaths tight; carpellate scales acuminate ....42. *C. scoparia*

5. Principal leaves 3-7 mm wide; leaf-sheaths loose; carpellate scales acute ....49. *C. tribuloides*

6. Body of perigynium broadest above the middle 7

6. Body of perigynium broadest near the middle or base 8

7. Perigynia 2.5-4 mm broad; carpellate scales long acuminate to aristate ....1. *C. alata*

7. Perigynia 1.5-2.5 mm broad; carpellate scales obtuse to acute ....2. *C. albolutescens*

8. Body of perigynium suborbicular, abruptly rounded to beak; perigynia winged to base ....18. *C. festucacea*

8. Body of perigynium narrowly ovate, gradually tapering to beak; perigynia

with wing abruptly narrowed below the middle ....13. *C. cristatella*

GROUP D

One species ....33. *C. leptalea*

GROUP E

1. Perigynia distinctly pubescent 2

1. Perigynia glabrous, scabrous, or minutely puberulent 4

 2. Perigynia 5-7 mm long; staminate spikelet 1-1.5 mm broad; carpellate spikelets 3-4(5) mm broad ....16b. C. debilis var. pubera

 2. Perigynia 2.5-4.5(5) mm long; staminate spikelet(s) 2.5-4 mm broad; carpellate spikelets 5-8 mm broad 3

3. Perigynia densely pubescent, with erect beak less than half as long as the body; staminate spikelets usually 2; leaves 1.5-5 mm wide ....32. *C. lanuginosa*

3. Perigynia scabrous or minutely pubescent, with curved or twisted beak half as long as or longer than the body; staminate spikelet 1; leaves 5-18 mm wide ....41. _C. scabrata_

   4. Bract of lowest spikelet long-sheathing (i.e., with a closed tubular sheath usually longer than 1 cm) 5

   4. Bract of lowest spikelet sheathless or very short-sheathing (sheath usually shorter than 1 cm) 17

5. Perigynia (4.5)5-10 mm long, with well-developed 2-toothed beak; terminal spikelet staminate throughout 6

5. Perigynia 2-5(6) mm long; beak, if present, either not 2-toothed _or_, if with 2 teeth, then terminal spikelet staminate below and carpellate above 8

   6. Perigynia minutely puberulent ....16b. C. debilis var. pubera

   6. Perigynia glabrous 7

7. Perigynia 6-10 mm long, the tip of the beak somewhat enlarged and conspicuously white-hyaline ....16a. _C. debilis_ var. _debilis_

7. Perigynia 4.5-7 mm long, the tip of the beak not enlarged and only inconspicuously white-hyaline ....16c. _C._ _debilis_ var. _rudgei_

8. Terminal spikelet staminate below, carpellate above 9

8. Terminal spikelet wholly staminate 12

9. Perigynia tapering into a triangular beak from half as long as to nearly as long as the body; leaf-sheaths and blades glabrous ....40. _C._ _prasina_

9. Perigynia with a short 2-toothed beak or beakless; leaf-sheaths and blades glabrous or pubescent 10

10. Leaf-sheaths and blades glabrous (lowermost sheaths may be more or less hispidulous); perigynia 2-3.5 mm long and 1-1.7 mm broad, beakless; lateral spikelets 2-3(4) mm broad ....23. _C._ _gracillima_

10. Leaf-sheaths and sometimes blades usually noticeably pubescent

(occasionally more or less
glabrous); perigynia 3.5-6 mm long
and 1.75-2.5 mm broad, with a short
to very short 2-toothed beak;
lateral spikelets 3-7 mm broad 11

11. Most carpellate scales with a definite awn often half or more the length of the body of the scale; perigynia (4)4.5-6 mm long, inflated, more or less loosely enveloping the achene ....15. _C. davisii_

11. Most carpellate scales acute, acuminate, or with an awn much shorter than the body of the scale; perigynia 3.5-4(5) mm long, not inflated, more or less closely enveloping the achene ....38. _C. oxylepis_

12. Perigynia tapering into a triangular beak from half as long as to nearly as long as the body ....40. _C. prasina_

12. Perigynia either beakless or with a beak very much shorter than the body 13

13. Larger perigynia 2-3.5(4) mm long, with few to many raised nerves 14

13. Larger perigynia 4-6 mm long, with impressed nerves 16

14. Carpellate spikelets slender-cylindric, 3-6 cm long and 2-3(4) mm broad, drooping or spreading; perigynia beakless ....23. _C_. _gracillima_

14. Carpellate spikelets short-cylindric, 1-3 cm long and (4)5-6 mm broad, erect or ascending; perigynia with a minute, straight or slightly bent beak 15

15. Staminate spikelet long-penuncled, its base surpassing the tip of the uppermost carpellate spikelet; leaves 1.5-3 mm wide ....11. C. crawei

15. Staminate spikelet sessile or short-peduncled, its base not surpassing the tip of the uppermost carpellate spikelet; leaves 3-10 mm wide ....24. _C_. _granularis_

16. Lowermost carpellate scales conspicuously awned; carpellate spikelets 3-15 flowered ....3. _C_. _amphibola_

16. Lowermost carpellate scales awnless or inconspicuously awned; carpellate spikelets 10-45 flowered ....19. _C_. _flaccosperma_

17. Terminal spikelet wholly staminate 18

17. Terminal spikelet staminate below, carpellate above 21

18. Perigynia scabrous; beak often outcurved ....41. _C_. _scabrata_

18. Perigynia glabrous or granular, not scabrous; beak straight or curved 19

19. Perigynia with a minute beak; the lowest carpellate spikelet often near the base of the plant; leaves 1.5-3 mm wide; culms 1-3 dm tall ....11. C. crawei

19. Perigynia with a conspicuous beak 1-2 mm long; the lowest carpellate spikelet well above the base of the plant; leaves 2.5-10 mm wide; culms 3-10 dm tall 20

20. Perigynia ca. 1.5 mm broad, not inflated, broadest below the middle, nerveless or few-nerved on faces, tapering into a triangular beak .....40. _C_. _prasina_

20. Perigynia 3-3.5 mm broad, inflated, broadest at or above the middle, conspicuously several-nerved on faces, abruptly narrowed to a conical beak ....29. _C. joorii_

21. Perigynia plump, nearly round in cross-section, with ca. 8-15 prominent nerves on faces; leaf-sheaths often pubescent (pubescence may be sparse); terminal spikelet mostly 1.5 cm or less long ..8. _C. caroliniana_

21. Perigynia 3-angled or more or less flattened in cross-section, not plump, essentially nerveless on faces (0-4 weak nerves) _or_ with more than 15 closely-spaced, fine nerves; leaf-sheaths glabrous; terminal spikelet 1.5-4 cm long 22

22. Carpellate scales whitish, with green midrib; perigynia tapering into a triangular beak to 2 mm long .40. _C. prasina_

22. Carpellate scales reddish-brown to brown, with green midrib; perigynia with a beak ca. 0.2 mm long 23

23. Perigynia broadly obovate; carpellate scales acute or mucronate, shorter than to as long as the perigynia; leaves 4-8 mm wide ....43. _C. shortiana_

23. Perigynia elliptic to obovate; carpellate scales acuminate or awned, mostly longer than the perigynia; leaves 1.5-4 mm wide ....7. _C. buxbaumii_

GROUP F

1. Perigynia shorter than the rough awned scales ....21. _C. frankii_

1. Perigynia much longer than the scales 2

   2. Style straight below; spikelets oblong-cylindric; beaks of perigynia mostly pointing toward summit of spikelet ....50. _C. typhina_

   2. Style strongly curved or bent near the base; spikelets oval or oblong-oval; beaks of perigynia widely spreading ....45. _C. squarrosa_

GROUP G

1. Staminate spikelets 2-4 on each flowering culm 2

1. Staminate spikelet only 1 on each flowering culm 3

   2. Perigynia more or less inflated, body thin (easily torn), with ca. 7-12 prominent nerves, more or less abruptly tapering into a slender beak ca. 2 mm long ....51. _C._ _vesicaria_

   2. Perigynia not inflated, body coriaceous (not easily torn), with more than 12 nerves (or nerves not discernible), gradually tapering into a beak ca. 1 mm long ....30. _C._ _lacustris_ var. _laxiflora_

3. Perigynia with 12-20 nerves 4

3. Perigynia with 10 or fewer nerves 5

   4. Perigynia inflated, the teeth erect, 0.5-1 mm long ....27. C. hystericina

   4. Perigynia not inflated, the teeth outwardly arching, 1.2-2 mm long ....9. C. comosa

5. Carpellate spikelets 14-20 broad; perigynia 6-9 mm long, the beak shorter than to about equalling the body; principal leaves 4-7 mm wide ....36. _C. lurida_

5. Carpellate spikelets 8-13 mm broad; perigynia 5-7 mm long, the beak equal to or longer than the body; principal leaves 2-4 mm wide ....5. _C. baileyi_

GROUP H

1. Perigynia narrowly lanceolate, 2.5-3.5 mm at broadest point, mostly with 25 or more nerves ....20. C. folliculata

1. Perigynia lanceolate-ovate, 4-8 mm at broadest point, mostly with fewer than 25 nerves 2

   2. Carpellate spikelets globose or nearly so; perigynia with a beak much shorter than the body 3

   2. Carpellate spikelets oblong to cylindric; perigynia with a beak nearly as long as to longer than the body 4

3. Perigynia generally (1)5-10(15) per spikelet, rounded at base, glabrous and shining ....28. *C. intumescens*

3. Perigynia generally (6)15-20(30) per spikelet, cuneate at base, dull and often hispidulous (especially toward base) ....25. *C. grayi*

4. Achene broader to much broader than long; perigynia widely spreading at maturity, the beak twice as long as the body ....22. *C. gigantea*

4. Achene longer than broad or about as broad as long; perigynia ascending or loosely spreading-ascending, the beak less than twice as long as the body 5

5. Staminate spikelet ca. 2.5 mm broad; carpellate spikelets somewhat longer than broad to as broad as long; perigynia loosely spreading-ascending; leaves 2-6 mm wide ....34. *C. louisianica*

5. Staminate spikelet(s) 3-5 mm broad; carpellate spikelets usually noticeably longer than broad; perigynia appressed-ascending; leaves 5-15 mm wide ....35. *C. lupulina*

1. *Carex alata* Torr. Figure 1

Rare in wet soil in a variety of habitats. Massachusetts to Michigan, Indiana, and Missouri, south to Florida and Texas.

2. *Carex albolutescens* Schw. Figure 2

Infrequent in moist to wet soil in a variety of habitats. Nova Scotia to Michigan, Missouri, and southeastern Kansas, south to Florida and Texas. (*C. longii* Mack; *C. straminea* of Mack., not Willd.)

3. *Carex amphibola* Steud. Figure 3

Common in moist to wet woods. New Brunswick to Minnesota and Nebraska, south to Florida and Texas. (*C. amphibola* vars. *rigida* (Bailey) Fern. and *turgida* Fern.; *C. grisea* of authors, not Wahl.)

4. *Carex atlantica* Bailey ssp. *atlantica* Figure 4

Infrequent in swamps, bogs, wet woods and thickets. Nova Scotia to Michigan, Indiana, and southern Illinois, south to Florida and Texas. (*C. atlantica* var. *incomperta* (Bickn.) Herm.; *C. incomperta* Bickn.)

This taxon belongs to a somewhat difficult group, the Stellulatae. Other species in this wetland group might possibly occur in Kentucky, and all will run to *C. atlantica* ssp. *atlantica* in this key. A taxonomic account of this group as it occurs in North America (north of Mexico) is given by Reznicek & Ball (1980), and reference to this paper is suggested.

5. *Carex baileyi* Britt. Figure 5

Infrequent in bogs, springy areas, and meadows. Nova Scotia to Quebec and southern Ontario, south to North Carolina and Tennessee.

6. *Carex bromoides* Willd. Figure 6

Occasional in swamps, low meadows, and wet woods. Nova Scotia to Wisconsin, south to Florida and Louisiana; Mexico.

7. *Carex buxbaumii* Wahl. Figure 7

Rare in open swampy and boggy areas. Newfoundland to Alaska, south to North Carolina, Georgia, Arkansas, Oklahoma, Utah, and California; Old World.

8. *Carex caroliniana* Schw. Figure 8

Common in moist to wet woods, meadows and ditches. New Jersey to Ohio, Missouri, and Oklahoma, south to South Carolina, Georgia, and Texas.

This species belongs to the group Virescentes, of which there are other members occurring in Kentucky. Any one of these species of normally dry to moist soil may occasionally be found in wet situations, and consultation of a more comprehensive manual is suggested.

9. Carex comosa Boott Figure 9.

There is a sheet of *C. comosa* (at the New York Botanical Garden) collected by C.W. Short, but no date or locational information is given. Possibly collected in Kentucky; also reported by Braun (1943) and by Mackenzie (1931-1935) as having been collected in Kentucky. To be expected here in marshes, swamps, and wet meadows and on margins of lakes and ponds. Nova Scotia to Quebec, South Dakota, and Nebraska, south to Florida and Texas; British Columbia to Idaho and California.

10. *Carex conjuncta* Boott Figure 10

Occasional in moist to wet woods. New York and New Jersey to Ohio, Nebraska, and South Dakota(?), south to Virginia and Kansas.

11. Carex crawei Dew.

Reported by Gunn (1959) from Bullitt County (specimen not seen) but apparently a misidentification since *C. crawei* is absent from his later Bullitt County checklist

(Gunn 1968b). Possibly in Kentucky; to be looked for in moist to wet meadows and prairie patches and on rock ledges, especially in calcareous areas. Nova Scotia to British Columbia, south to New Jersey, Georgia, Tennessee, Oklahoma, and Utah.

Carex tetanica var. meadii (Dew.) Bailey (C. meadii Dew.), found most often in Kentucky in limestone glades and prairies and only occasionally collected from wet soil, will run to C. crawei in this key. Carex crawei has perigynia that are straight-beaked, broadest at the middle or below and often resinous-dotted; the perigynia of C. tetanica var. meadii have a bent beak, are broadest above the middle, and are without resin dots.

12. Carex crinita Lam. Figure 11

Common in moist to wet soil in a variety of habitats. Newfoundland to Manitoba, south to South Carolina, Georgia, Louisiana, and Texas. (C. crinita var. brevicrinis Fern.)

Reference: Standley 1983.

13. Carex cristatella Britt. Figure 12

Infrequent in swamps, wet woods, and wet meadows. New Hampshire to Quebec and Alberta, south to North Carolina, Kansas, and Nebraska.

14. Carex crus-corvi Kunze Figure 13

Frequent in swamps, marshes, and ditches. Ohio and Michigan to Nebraska, south to Florida and Texas.

15. *Carex davisii* Schw. & Torr. Figure 14

Frequent in moist to wet woods, thickets and ditches. Vermont and Quebec to North Dakota and Nebraska, south to Maryland, Tennessee, Missouri, Oklahoma, and Texas.

16. *Carex debilis* Michx.

a. var. *debilis* Figure 15

Occasional in swampy woods and wet meadows. Massachusetts to Indiana and Missouri, south to Florida and Texas.

b. var. pubera Gray Figure 16

Rare in low woods and wet meadows. Pennsylvania to Georgia (*C. allegheniensis* Mack.)

c. var. *rudgei* Bailey Figure 17

Infrequent in swampy woods, moist ravines, and wet meadows. Newfoundland to Ontario, south to North Carolina, Georgia, and Missouri. (*C. flexuosa* Muhl.)

17. *Carex decomposita* Muhl. Figure 18

Infrequent in swamps. New York to Michigan and Missouri, south to Florida and Texas.

18. *Carex festucacea* Willd. Figure 19

Common in swamps, wet woods, and wet meadows. Massachusetts to Ontario, Michigan, Iowa, and North Dakota, south to Florida, Louisiana, and Oklahoma.

19. *Carex flaccosperma* Dew. Figure 20

Common in moist to wet woods, swamps, and wet meadows. Massachusetts to southern Ontario, Ohio, and Missouri, south to Florida and Texas. (*C. flaccosperma* var. *glaucodea* (Tuckerm.) Kuek.; *C. glaucodea* Tuckerm.)

20. Carex folliculata L.

Listed by Short & Peter (1834) as occurring in Kentucky (no county given), and possibly to be found here in wet woods and swamps. Newfoundland to Wisconsin, south to Florida and Texas.

21. *Carex frankii* Kunth Figure 21

Common in wet woods, meadows, marshes, and ditches and on margins of lakes and ponds. New York to southern Ontario, Michigan, Nebraska, and Kansas, south to Florida and New Mexico; South America.

22. *Carex gigantea* Rudge Figure 22

Rare in swamps and wet woods. Delaware to southern Indiana, southern Illinois, southeastern Missouri, and Oklahoma, south to Florida and Texas.

23. *Carex gracillima* Schw. Figure 23

Frequent in wet woods and seep areas. Newfoundland to Manitoba and North Dakota, south to North Carolina, Georgia, and Missouri.

24. *Carex granularis* Willd. Figure 24

Common in moist to wet soil in a variety of habitats. Nova Scotia to Saskatchewan, south to Florida and Texas. (*C. granularis* vars. *haleana* (Olney) Porter and *recta* Dew.; *C. haleana* Olney; *C. rectior* Mack.)

25. *Carex grayi* Carey Figure 25

Common in wet woods and ditches. Southwestern Quebec to Iowa and Kansas, south to South Carolina, Mississippi, and Oklahoma. (*C. grayi* var. *hispidula* Bailey)

26. *Carex gynandra* Schw. Figure 26

Infrequent in moist to wet soil in a variety of habitats. Newfoundland to Wisconsin, south to Florida and Louisiana. (*C. crinita* var. *gynandra* (Schw.) Schw. & Torr.)

Sometimes treated as a variety of *C. crinita*; evidence for its recognition as a distinct species is given by Standley (1983).

27. Carex hystericina Willd. Figure 27

Reported by Braun (1943) and by Mackenzie (1931-1935) as having been collected in Kentucky, and to be expected here in swamps and wet meadows. Nova Scotia to British Columbia, south to Virginia, Georgia, Arkansas, Texas, and California.

The specific epithet is sometimes spelled "hystricina."

28. *Carex intumescens* Rudge Figure 28

Common in wet woods. Newfoundland to Manitoba and South Dakota, south to Florida and Texas.

29. *Carex joorii* Bailey Figure 29

Rare in wet woods and swamps. Maryland to Florida and Texas, north in the interior to Missouri and Kentucky.

30. *Carex lacustris* Willd. var. *laxiflora* Dew. Figure 30

Frequent in ditches, swamps, and marshes and on margins of lakes and ponds. New Jersey to southern Ontario, Wisconsin, Iowa, and Nebraska, south to Florida and Texas. (*C. hyalinolepis* Steud.)

Carex lacustris var. *laxiflora* has perigynia with many finely impressed nerves (actual nerves not always discernible) or a few elevated nerves, and the adaxial sides of the lower leaf-sheaths of the fertile culms only rarely become fibrillose. The typical variety, var.

lacustris, has many elevated nerves, and the lower leaf-sheaths of the fertile culms commonly break and become fibrillose adaxially. This latter variety is known from the southern borders of Ohio, Indiana, and Illinois and is possibly in Kentucky. Nova Scotia to Alberta, south to Virginia, Kansas, and Nebraska. (*C. riparia* var. *lacustris* (Willd.) Kuek.)

31. *Carex laevivaginata* (Keuk.) Mack. Figure 31

Frequent in swamps, wet woods and seep areas. Maine to Minnesota, south to Florida, Tennessee, and Oklahoma.

32. *Carex lanuginosa* Michx. Figure 32

Rare in wet meadows and open swampy areas and on margins of lakes and ponds. Newfoundland to British Columbia and Alaska, south to Virginia, Arkansas, Texas, and California. (*C. lasiocarpa* Ehrh. var. *latifolia* (Boeck.) Gilly)

33. *Carex leptalea* Wahl. Figure 33

Infrequent in bogs, damp open woods, wet meadows, and wet limestone ledges. Newfoundland to Alaska, south to Florida, Texas, New Mexico, Utah, and California. (*C. leptalea* var. *harperi* (Fern.) Stone)

34. *Carex louisianica* Bailey Figure 34

Frequent in swamps, bogs, and wet woods. New Jersey and the District of Columbia to southern Indiana, southern Illinois, Missouri, and Oklahoma, south to Florida and Texas.

35. *Carex lupulina* Willd. Figure 35

Common in swampy forests, marshes, ditches, moist fields, and thickets. Nova Scotia to Minnesota and Nebraska, south to Florida and Texas. (*C. lupuliformis* Sartw.)

36. *Carex lurida* Wahl. Figure 36

Common in swampy forests, bogs, ditches, and meadows and on margins of lakes and ponds. Nova Scotia to Minnesota, south to Florida and Texas; Mexico.

37. *Carex muskingumensis* Schw. Figure 37

Occasional in swamps and wet woods. Southern Ontario to Manitoba, south to Kentucky, Kansas, and Oklahoma.

38. *Carex oxylepis* Torr. & Hook. Figure 38

Infrequent in moist to wet woods. Virginia to Florida and Texas, north in the interior to southern Illinois, southeastern Missouri, and Kentucky.

39. Carex prairea Dew.

There is a sheet of *C. prairea* (at the New York Botanical Garden) collected by C.W. Short in 1836, with no locational information given (possibly collected in Kentucky). To be looked for in wet meadows, fens, and other wet habitats. Nova Scotia to British Colulmbia, south to New Jersey, West Virginia, Ohio, Illinois, Nebraska, and Idaho. (*C. prarisa*, original spelling of the epithet, later corrected to *C. prairea*, fide Mackenzie (1931-1935))

40. *Carex prasina* Wahl. Figure 39

Occasional in moist to wet woods and on stream banks. Maine to Michigan and Illinois, south to North Carolina, Georgia, Tennessee, and Arkansas.

41. *Carex scabrata* Schw. Figure 40

Infrequent in moist to wet, usually shaded ground, especially springy places in woods. New Brunswick to Michigan, south to South Carolina, Georgia, Tennessee, and Missouri.

42. *Carex scoparia* Willd. Figure 41

Frequent in marshes, wet fields, and ditches. Newfoundland to British Columbia, south to South Carolina, Georgia, Tennessee, Arkansas, Arizona, Idaho, and Oregon.

43. *Carex shortiana* Dew. Figure 42

Frequent in swamps, meadows, and ditches and on margins of lakes and ponds. Pennsylvania and southern Ontario to Iowa and Kansas, south to Virginia, Tennessee, Arkansas, and Oklahoma.

Carex x deamii Herm., a hybrid between C. shortiana and C. typhina, has been collected in Kenton County (Braun 1943). Similar to C. shortiana but with broader spikelets (7-8 mm vs. 4-5 mm in C. shortiana) and perigynia with longer beaks (1-1.5 mm vs. 0.2 mm in C. shortiana). Steyermark (1963) notes that plants resembling C. x deamii have been found in Missouri growing with C. shortiana and C. squarrosa.

44. Carex socialis Mohlenbrock & Schwegman Figure 43

A local species of river terraces, floodplains, swamps, and moist to wet woods. Southern Illinois, southeastern Missouri, and western Kentucky. For original description see Brittonia 21:77-79. 1969.

This species belongs to a normally dry-to-mesic woodland group of sedges, the Bracteosae. Several species in this group occur in Kentucky, and many of them are quite common. All species in this group will be identified as C. socialis in this key. In general, C. socialis may be distinguished from them by its very narrow (0.7-0.8 mm broad) perigynia. Reference to Mohlenbrock (1975) will further serve to distinguish *C. socialis* from other species in the Bracteosae (e.g., *C. rosea* and *C. sparganioides*) that occasionally are collected in wet habitats.

Reference: Mohlenbrock & Schwegman 1969.

45. *Carex squarrosa* L. Figure 44

Common in swamps, wet woods, meadows, ditches, and thickets. Southwestern Quebec to Minnesota and Nebraska, south to South Carolina, Georgia, Tennessee, Louisiana, and Oklahoma.

46. *Carex stipata* Willd. Figure 45

Frequent in moist to wet soil in a variety of habitats. Newfoundland to Alaska, south to Florida and California; Old World. (*C. stipata* var. *maxima* Chapm.; *C. uberior* (Mohr) Mack.)

47. *Carex stricta* Lam. var. *stricta* Figure 46

Rare in marshes, ditches, and seep areas. Nova Scotia to North Dakota, south to Georgia, Texas, Colorado, and Wyoming. (*C. stricta* var. *strictior* (Dew.) carey; *C. strictior* Dew.)

Carex stricta may be segregated into two varieties. The typical variety, reported from Kentucky, has the ligule longer than wide, the lower leaf-sheaths fibrillose, and the lower carpellate spikelets more or less remote. Carex stricta var. elongata (Boeck.) Gl. (C. emoryi Dew.) has the ligule as wide as or wider than long, the lower leaf-sheaths not fibrillose, and the lower carpellate spikelets often overlapping; it is wide-ranging in central and eastern North America and is to be looked for in Kentucky.

48. Carex torta Boott Figure 47

Frequent along stream banks. Nova Scotia to Minnesota, south to North Carolina, Georgia, Tennessee, and Arkansas.

49. Carex tribuloides Wahl. Figure 48

Common in moist to wet woods, meadows, and ditches. Nova Scotia to Minnesota, Nebraska, and Idaho, south to Florida and Texas.

50. Carex typhina Michx. Figure 49

Common in swamps and wet woods. Maine and southwestern Quebec to Wisconsin, south to Florida and Texas.

51. Carex vesicaria L. Figure 50

Rare in wet soil in a variety of habitats. Newfoundland to British Columbia, south to Delaware, Kentucky, Missouri, Colorado, New Mexico, Arizona, and California; Old World.

A wide-ranging and polymorphic taxon, of which a number of varieties are sometimes recognized. Plants in our area have been called var. monile (Tuckerm.) Fern.

_52_. _Carex vulpinoidea_ Michx. Figure 51

Common in moist to wet, usually open soil in a variety of habitats. Newfoundland to British Columbia, south to Florida, Arizona, and Oregon; introduced into Europe. (_C_. _annectens_ (Bickn.) Bickn. and var. _xanthocarpa_ (Bickn.) Wieg.; _C_. _vulpinoidea_ var. _ambigua_ Boott; _C_. _brachyglossa_ Mack.; _C_. _triangularis_ Boeck.)

LITERATURE CITED

Braun, E.L. 1943. An annotated catalog of spermatophytes of Kentucky. Published by the author, Cincinnati.

Braun, E.L. 1967. The Monocotyledoneae: Cat-Tails to Orchids. Volume 1 of the Vascular Flora of Ohio. Ohio State University Press, Columbus.

Gleason, H.A. and A. Cronquist. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Van Nostrand Reinhold Co., New York.

Gunn, C.R. 1959. A flora of Bernheim Forest, Bullitt County, Kentucky. Castanea 24: 61-98

Gunn, C.R. 1968. A check list of the vascular plants of Bullitt Count, Kentucky. Castanea 33: 89-106.

Mackenzie, K.K. 1931-1935. Cyperaceae: Cariceae. North American Flora 18:1-478.

Mohlenbrock, R.H. 1975. Guide to the Vascular Flora of Illinois. Southern Illinois University Press, Carbondale.

Mohlenbrock, R.H. and J. Schwegman. 1969. A new species of Carex Sect. Bracteosae. Brittonia 21:77-79.

Reznicek, A.A. and P.W. Ball. 1980. The taxonomy of Carex section Stellulatae in North America north of Mexico. Contr. Univ. Michigan Herb. 14:153-203.

Short, C.W. and R. Peter. 1834. A supplementary catalogue of the plants of Kentucky. The Transylvania Journal of Medicine and the Associate Sciences 7:598-600. (Reprinted 1978 in *Scientific publications of Charles Wilkins Short*, edited by R.L. Stuckey, Arno Press, New York.)

Standley, L.A. 1983. A clarification of the status of *Carex crinita* and *C. gynandra* (Cyperaceae). Rhodora 85:229-241.

Steyermark, J.A. 1963. *Flora of Missouri*. Iowa State Univ. Press, Ames.

Voss, E.G. 1972. *Michigan Flora: Part 1 Gymnosperms and Monocots*. Cranbrook Institute of Science, Bloomfield Hills, Michigan.

Figure 1. CAREX ALATA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

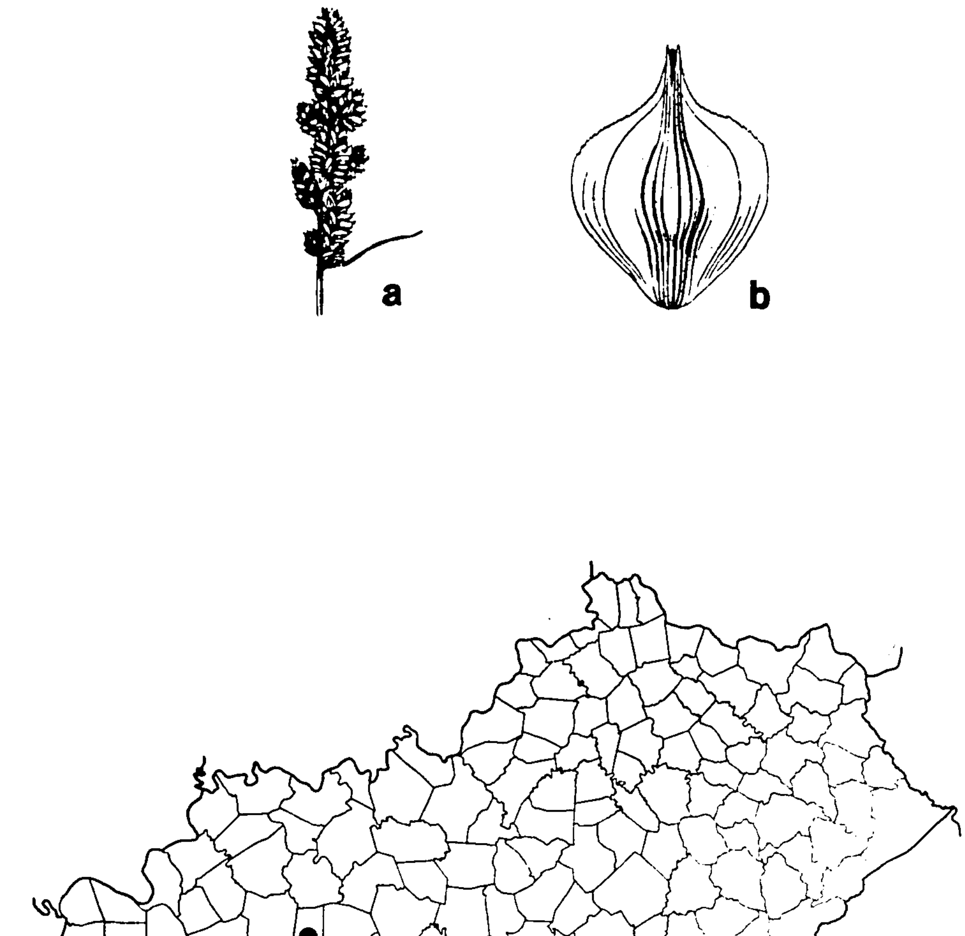
a
b
c

Figure 2. CAREX ALBOLUTESCENS (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

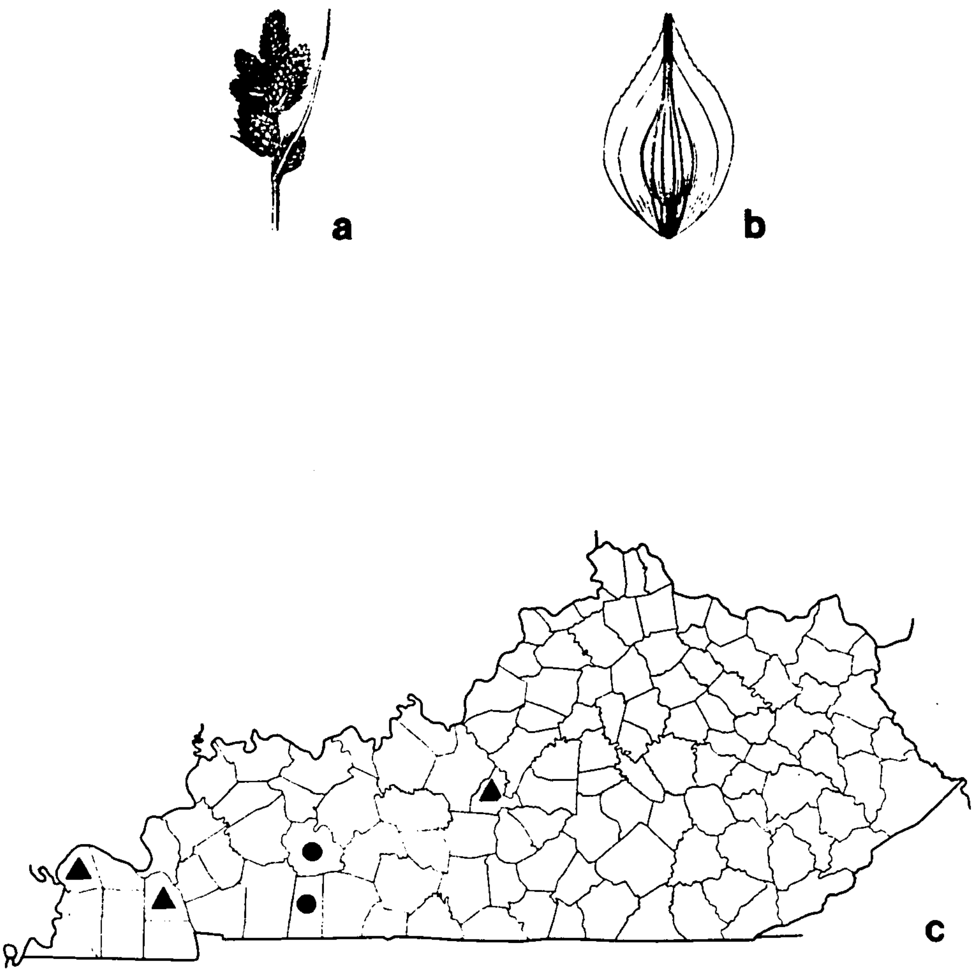
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Figure 3. CAREX AMPHIBOLA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

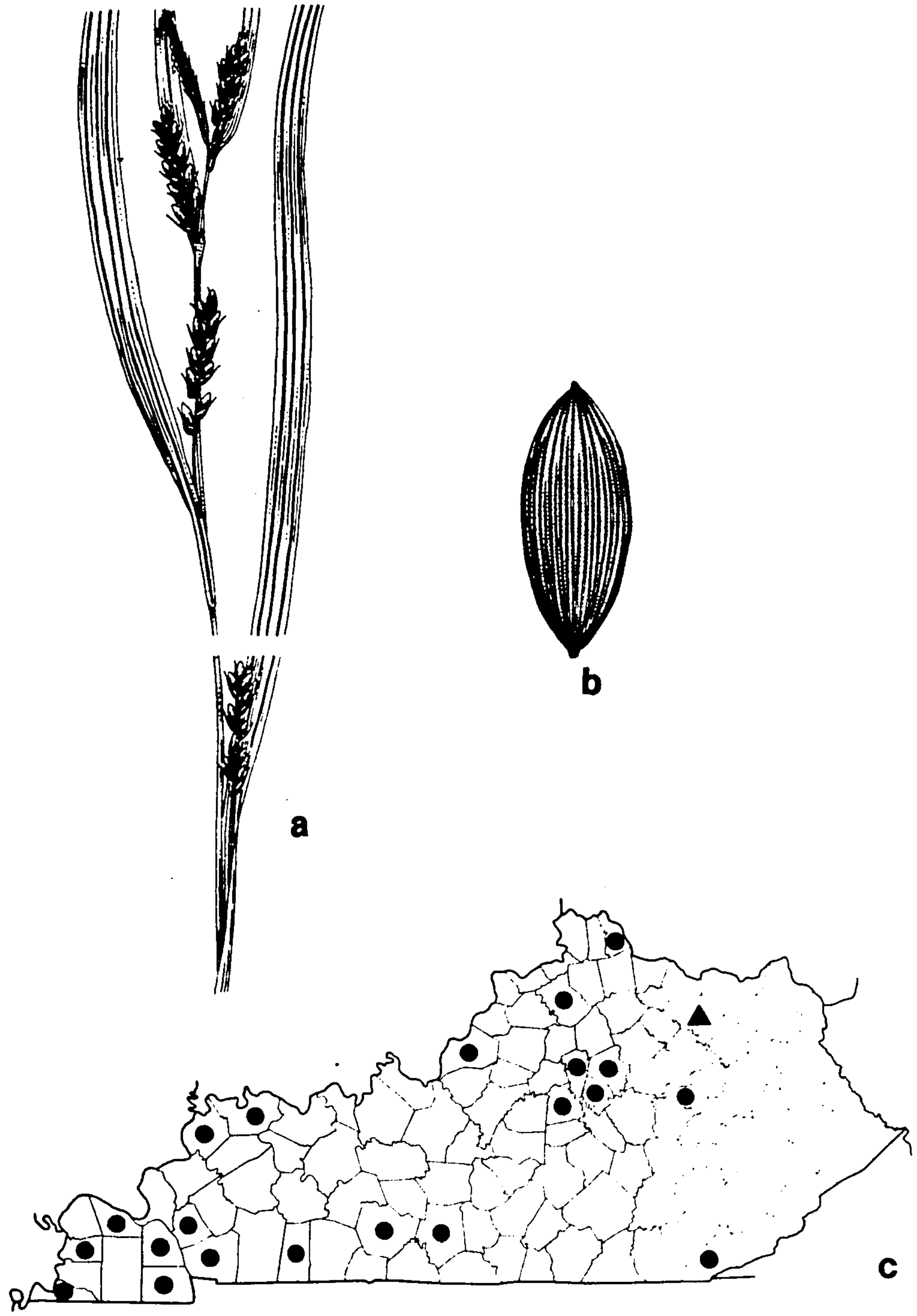
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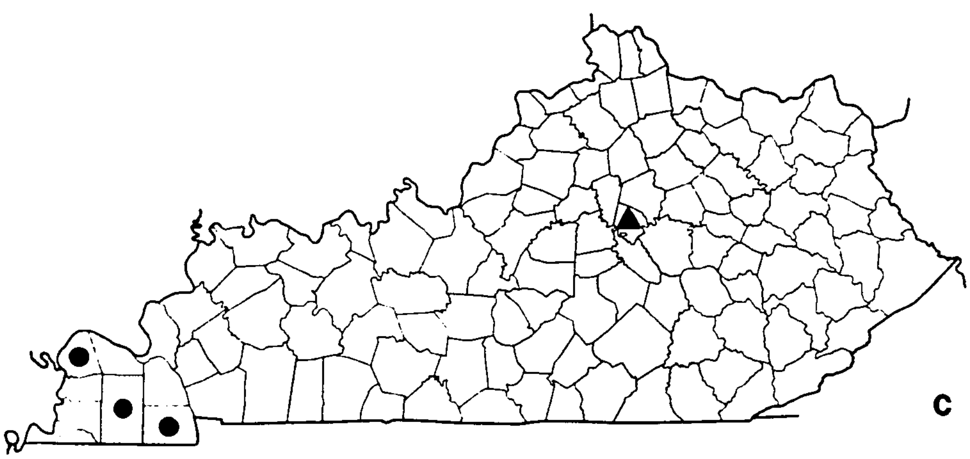
Figure 4. CAREX ATLANTICA ssp. ATLANTICA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

a

b



c

Figure 5. CAREX BAILEYI (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

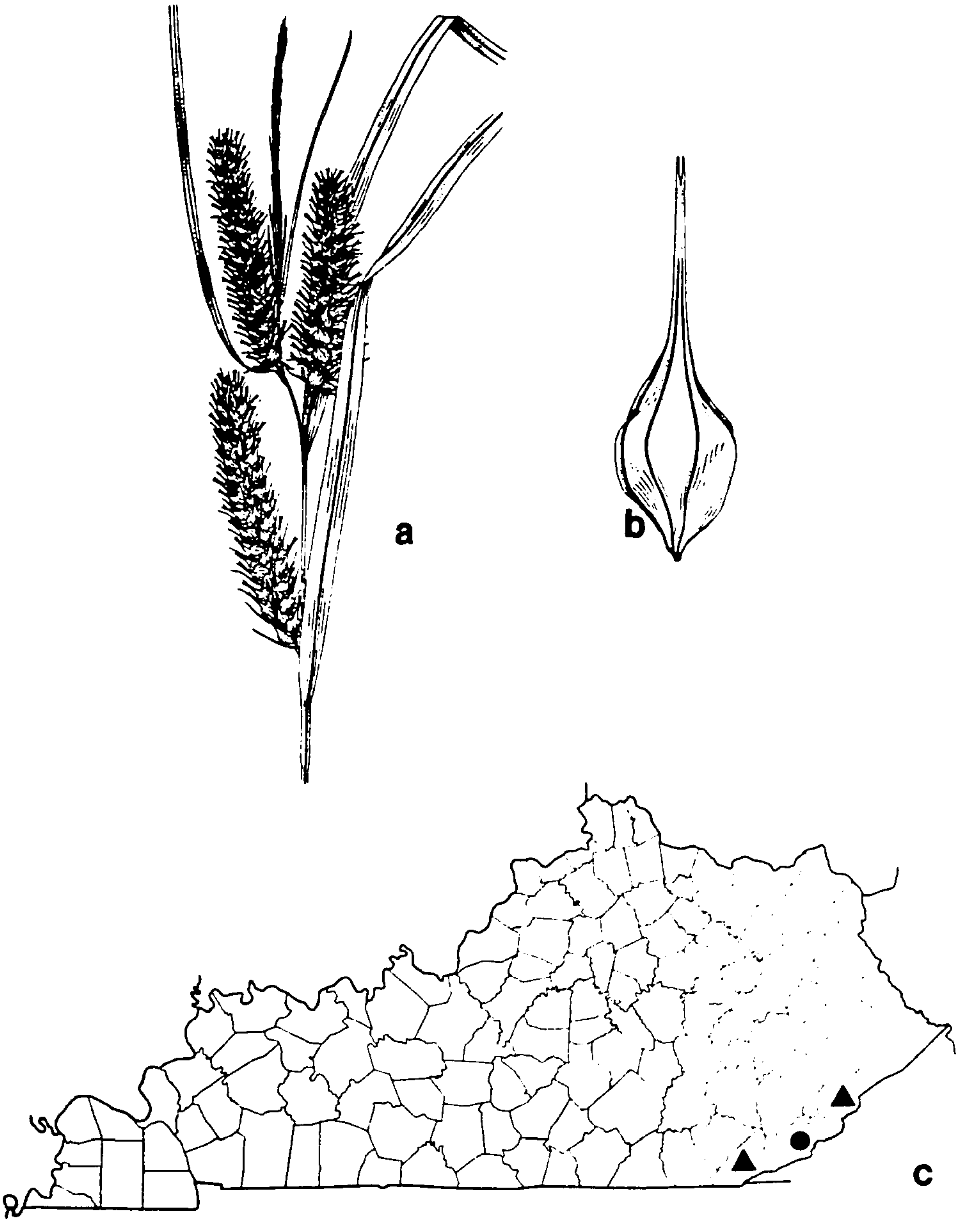
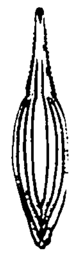

a
b
c

Figure 6. CAREX BROMOIDES (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.


a


b

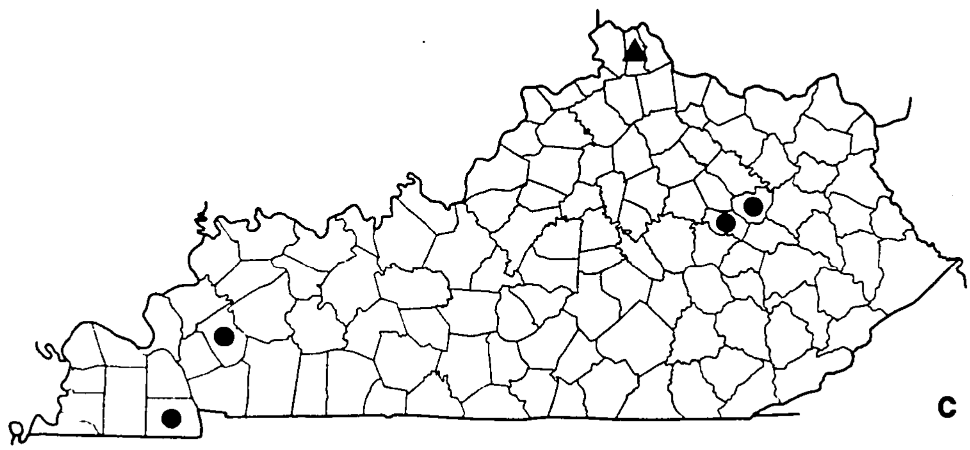

c

Figure 7. CAREX BUXBAUMII (a) inflorescence, X1; (b) scale, X8; (c) perigynium, X8; (d) distribution map.

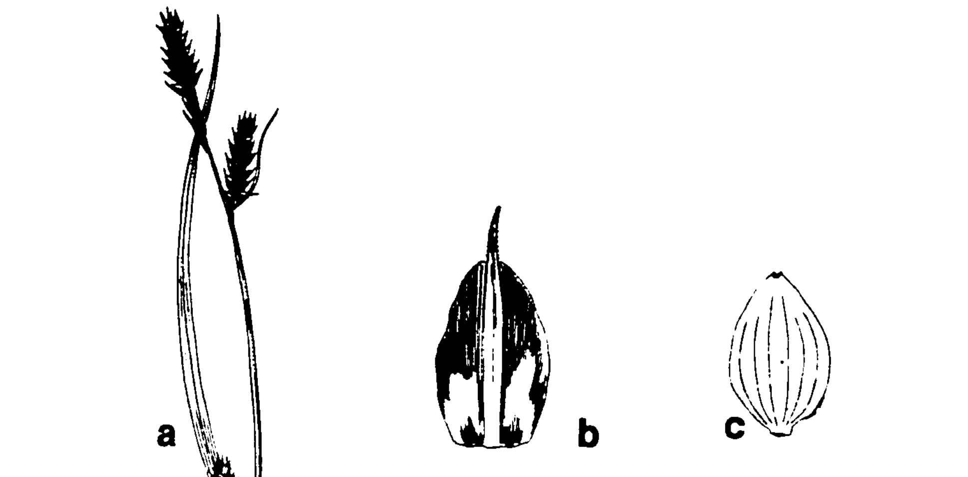
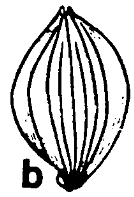

a
b
c
d

Figure 8. CAREX CAROLINIANA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.


a


b

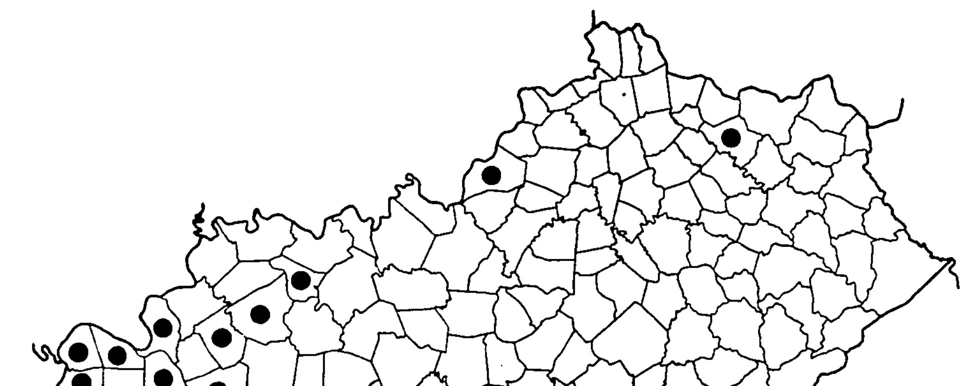

c

Figure 9. CAREX COMOSA (a) inflorescence, X1; (b) perigynium, X8;


a
b

Figure 10. CAREX CONJUNCTA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

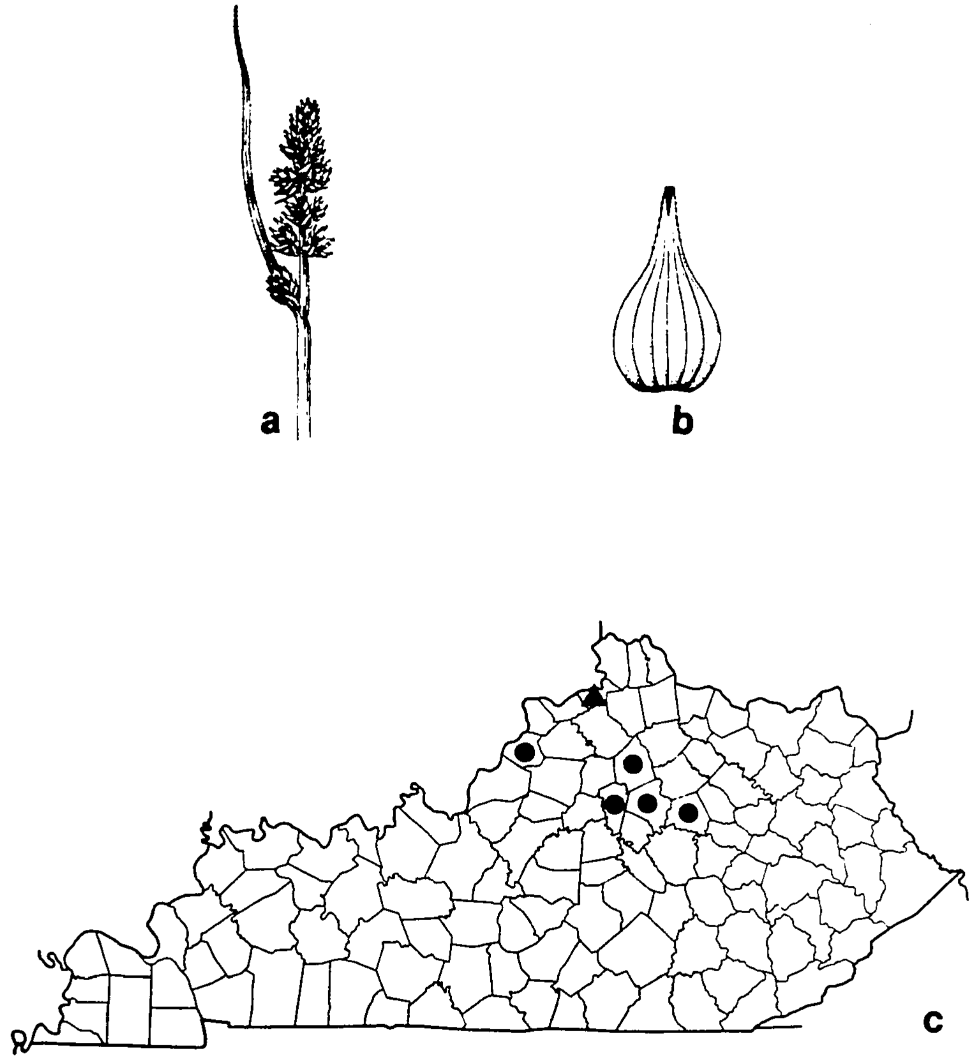

a
b
c

Figure 11. CAREX CRINITA (a) inflorescence, X1; (b) scale, X8; (c) perigynium, X8; (d) distribution map.

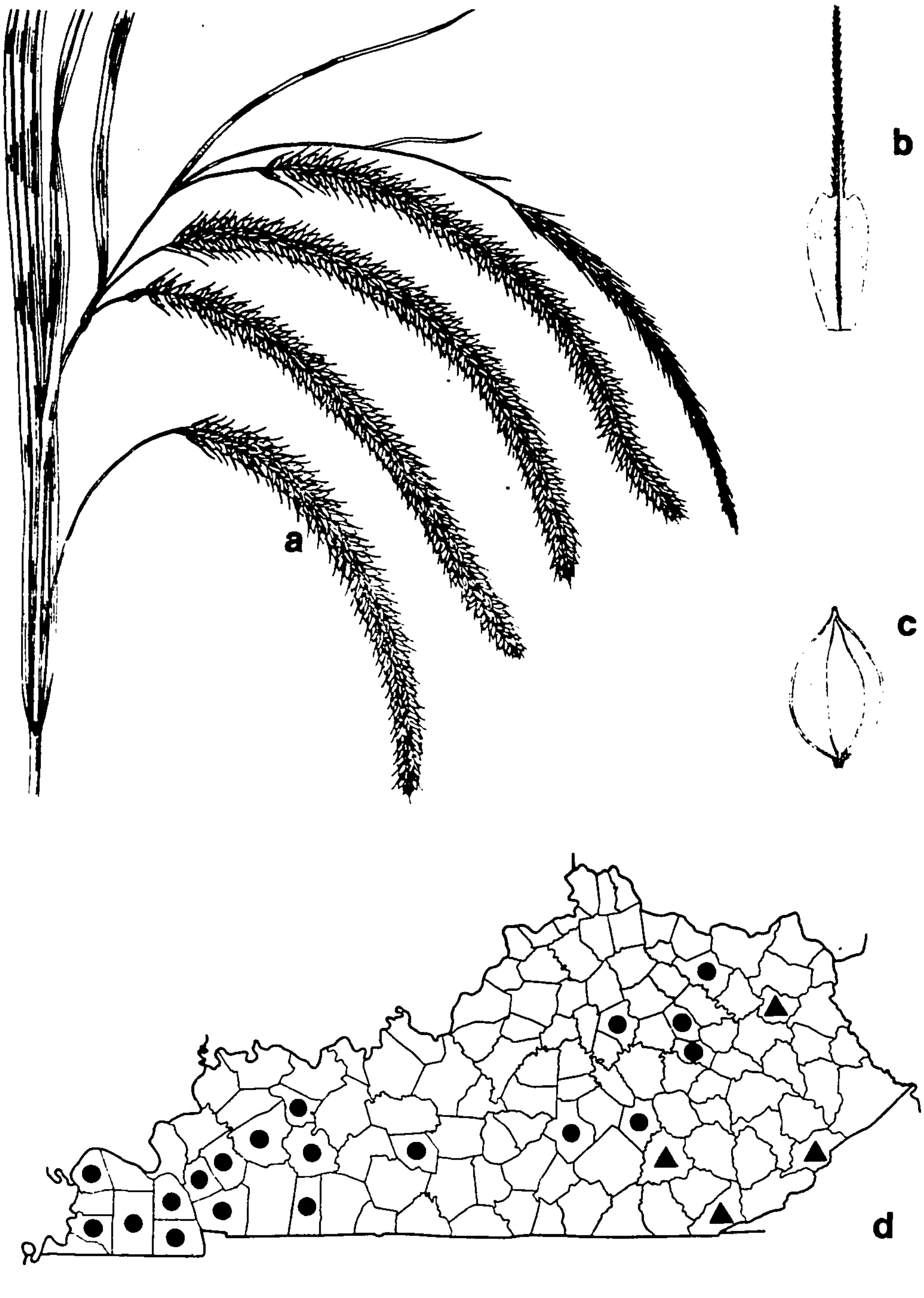

a
b
c
d

Figure 12. CAREX CRISTATELLA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

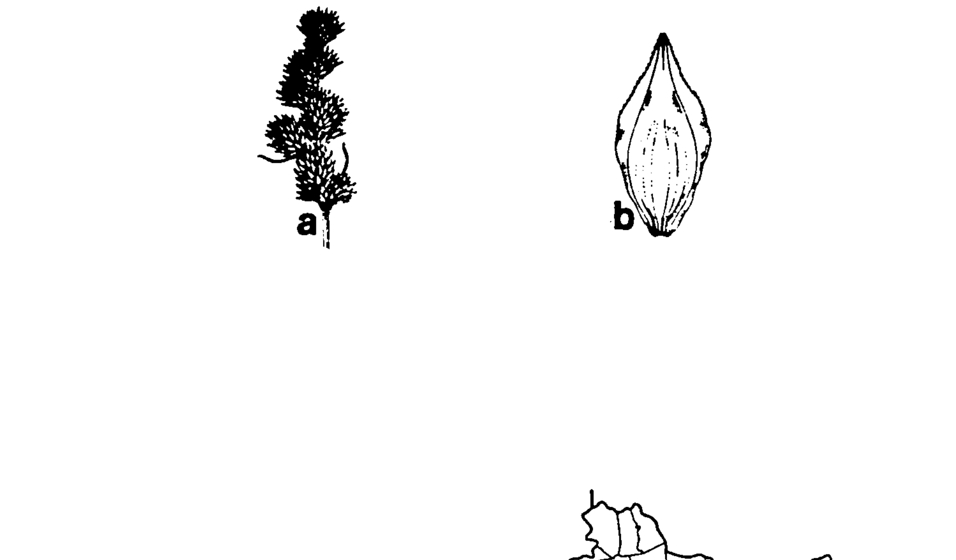
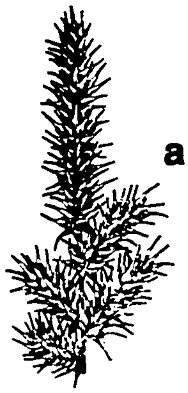
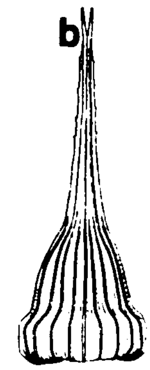

a
b
c

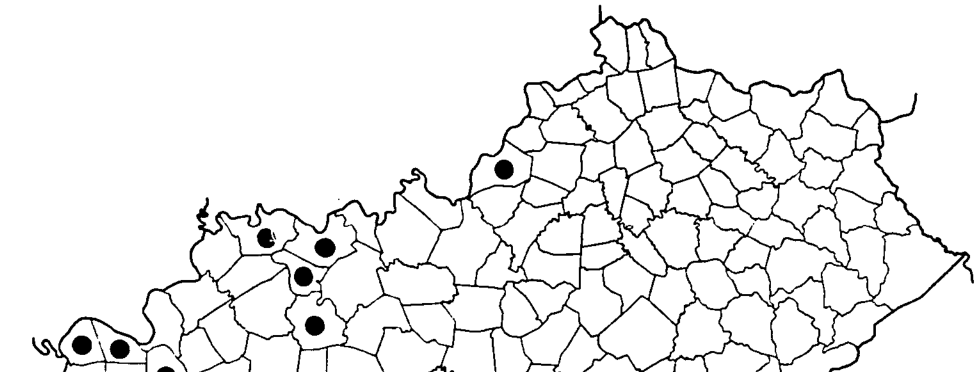
Figure 13. CAREX CRUS-CORVI (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.



a



b



c

Figure 14. CAREX DAVISII (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

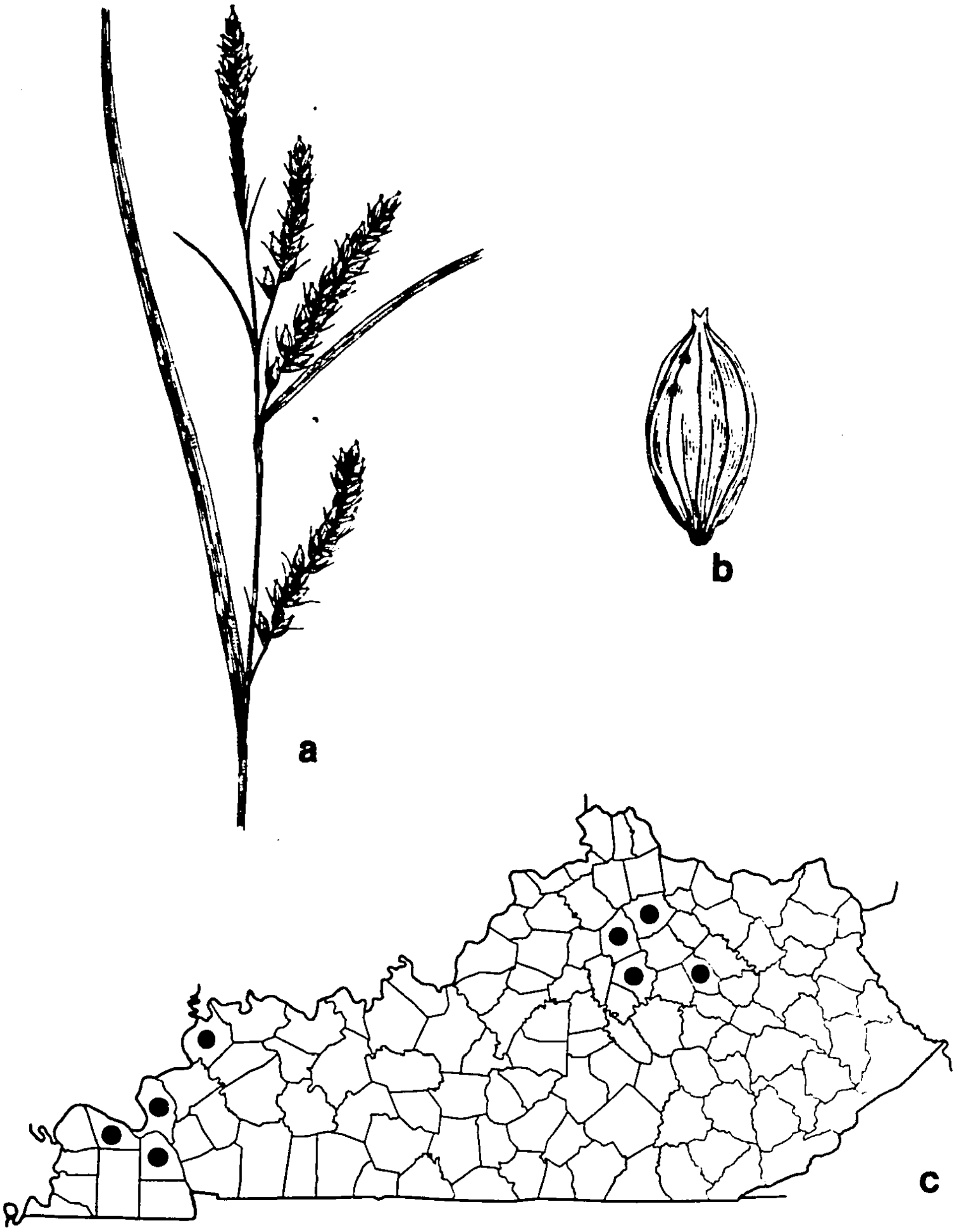

a
b
c

Figure 15. CAREX DEBILIS var. *debilis* (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

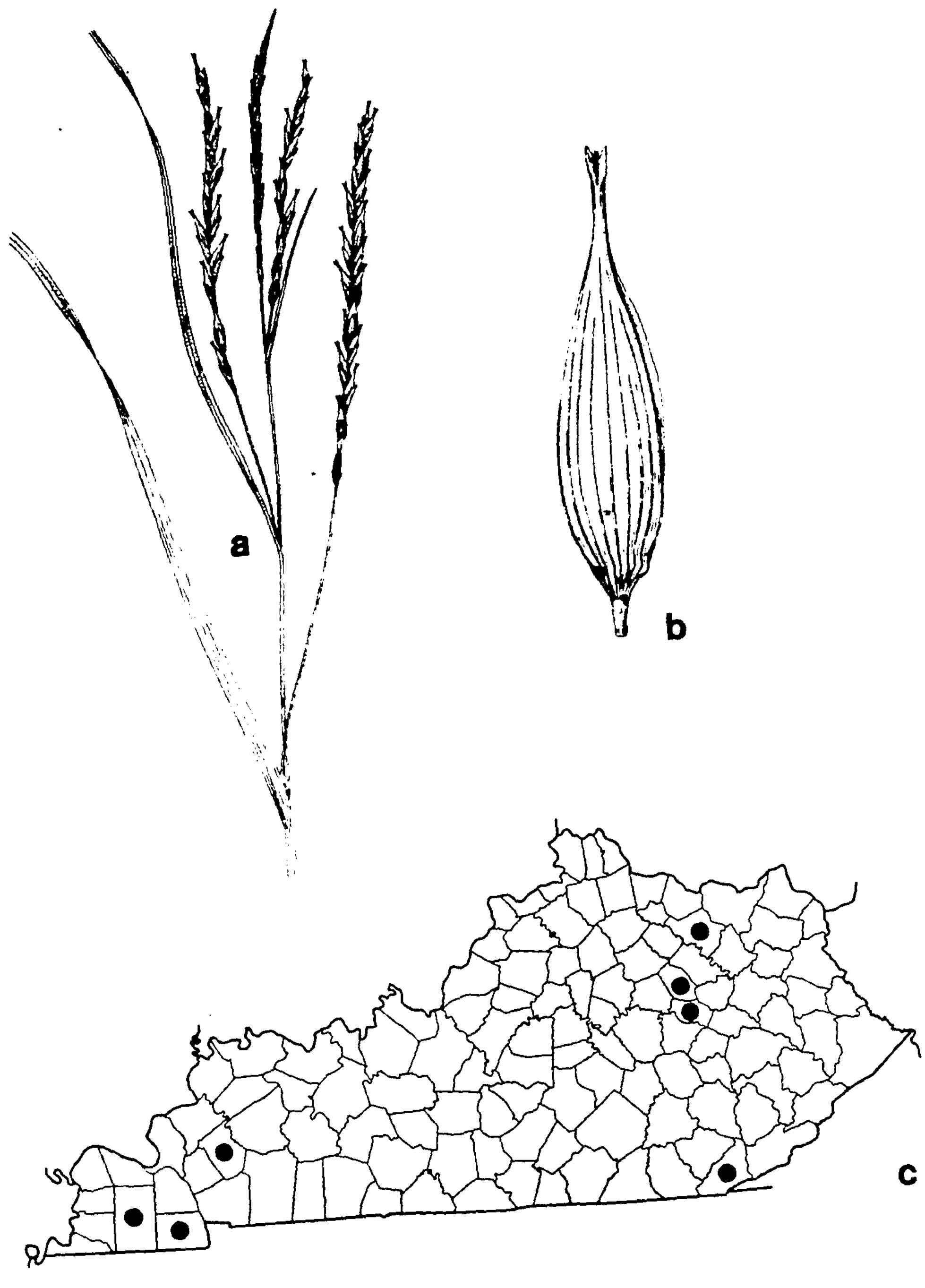
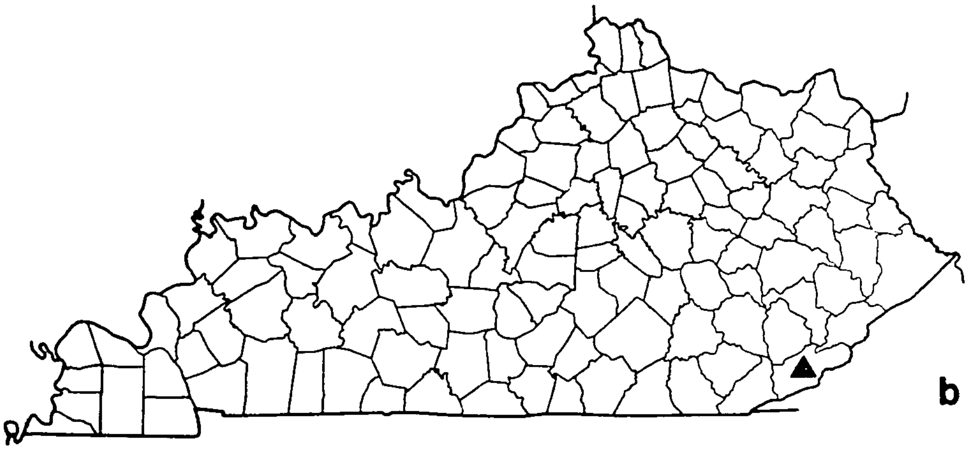

a
b
c

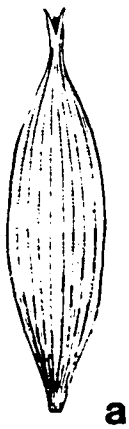
Figure 16. CAREX DEBILIS var. *pubera* (a) perigynium, X8; (b) distribution map.

a

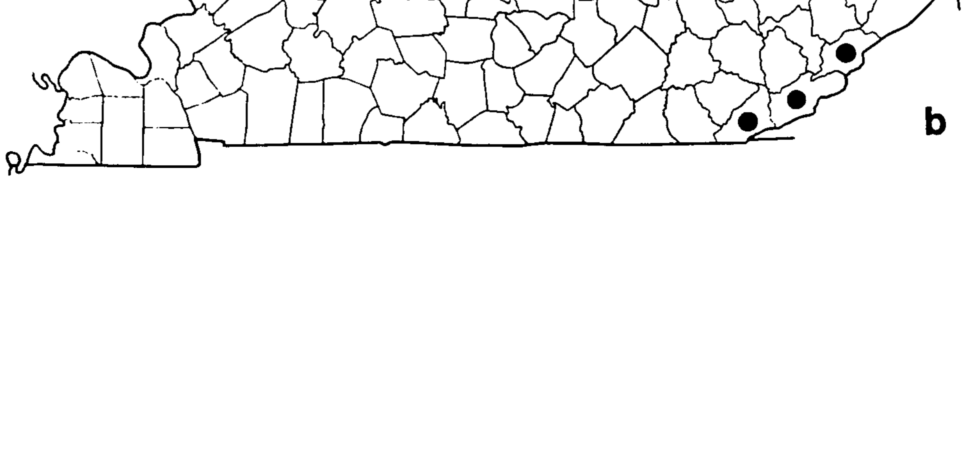


b

Figure 17. CARAEX DEBILIS var. *rudgei* (a) perigynium, X8;
(b) distribution map.



a



b

Figure 18. CAREX DECOMPOSITA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

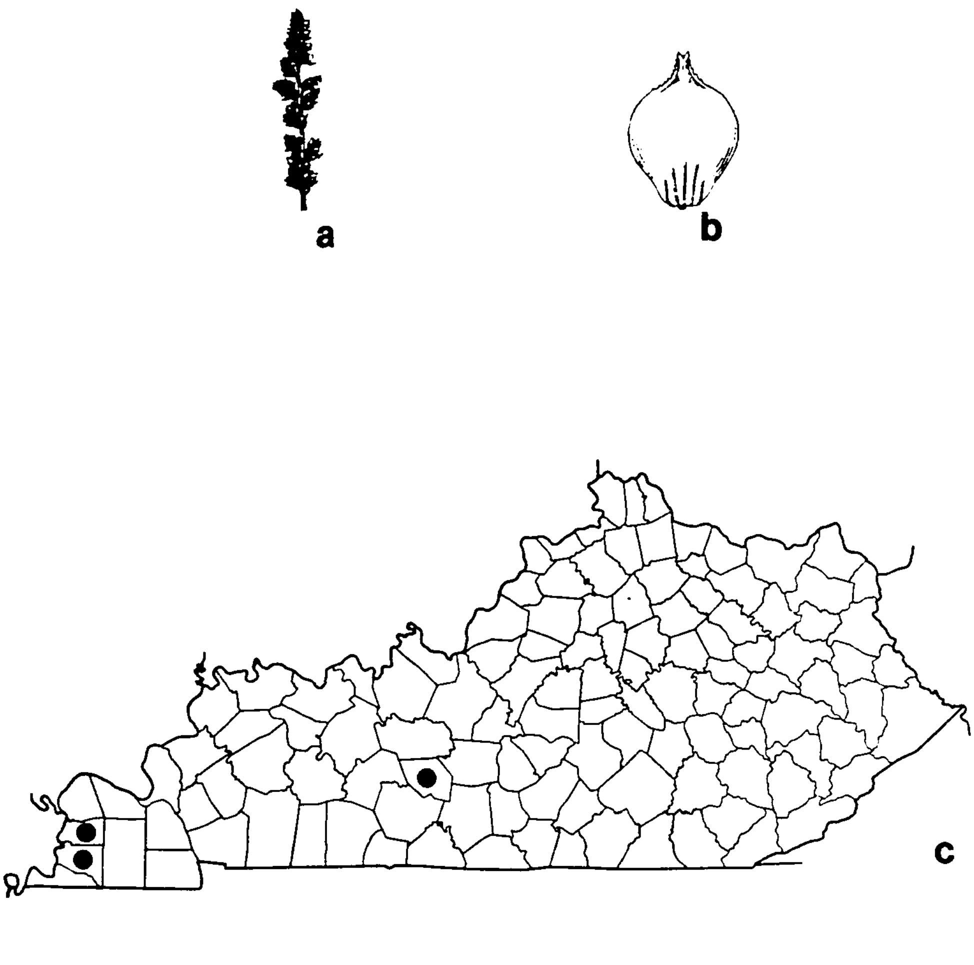

a
b
c

Figure 19. CAREX FESTUCACEA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

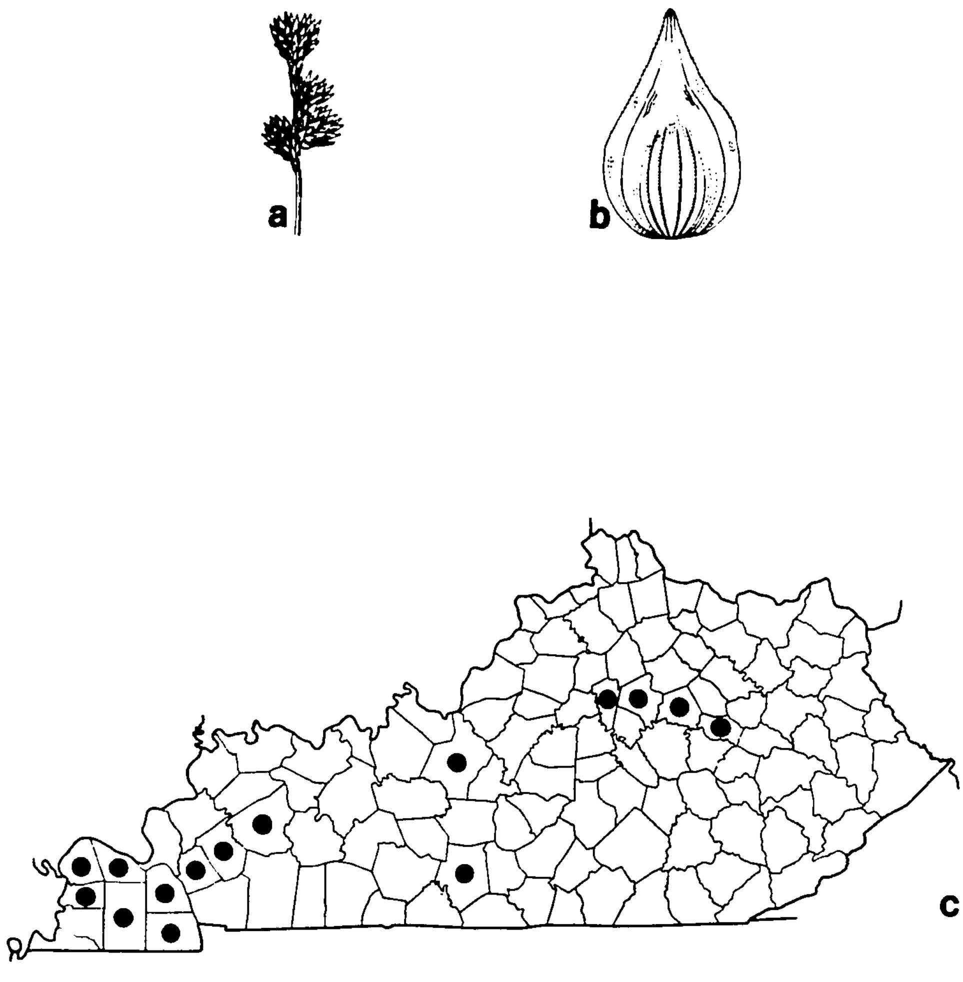

a
b
c

Figure 20. CAREX FLACCOSPERMA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

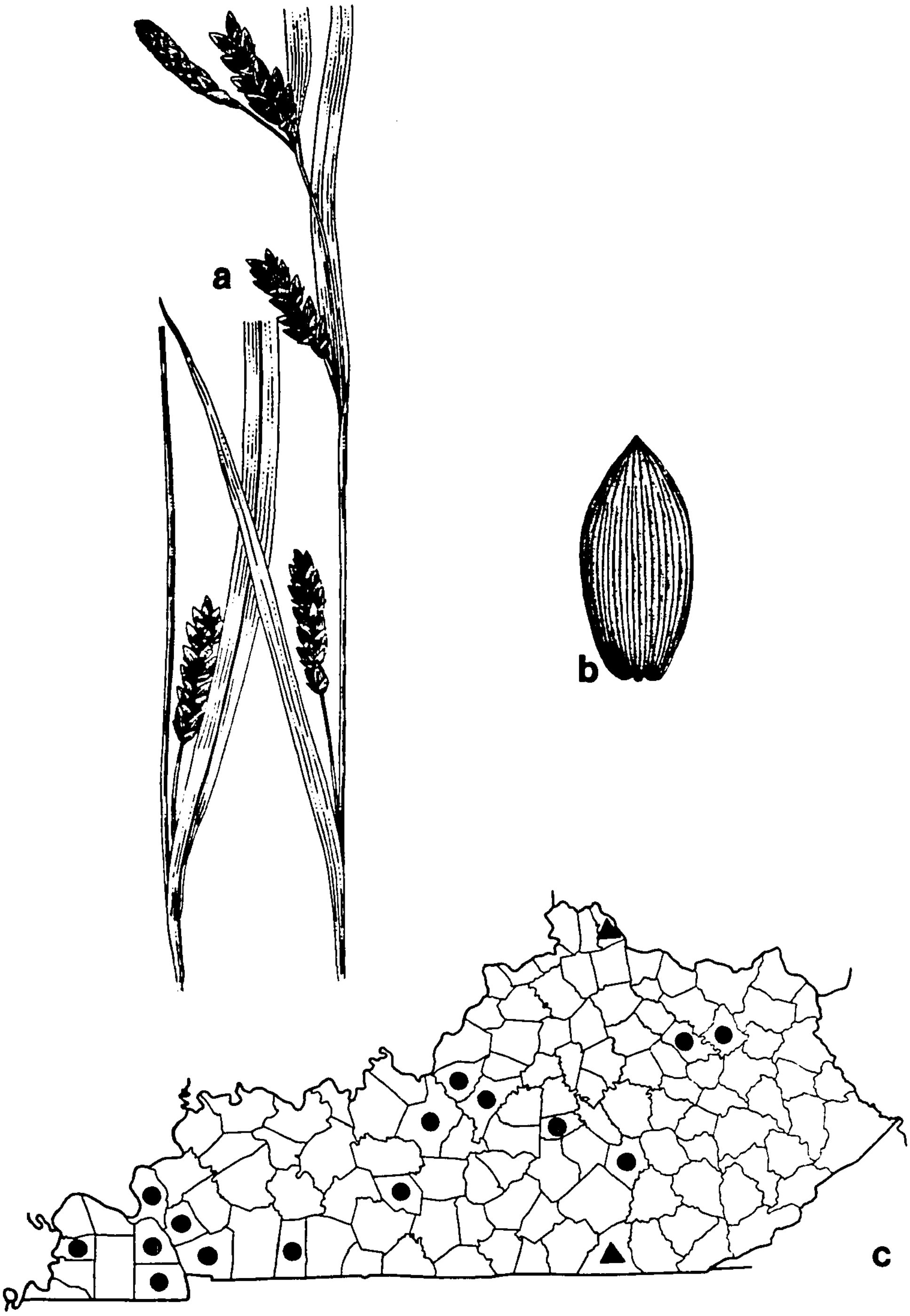

a
b
c

Figure 21. CAREX FRANKII (a) inflorescence, X1; (b) scale X8; (c) perigynium, X8; (d) distribution map.

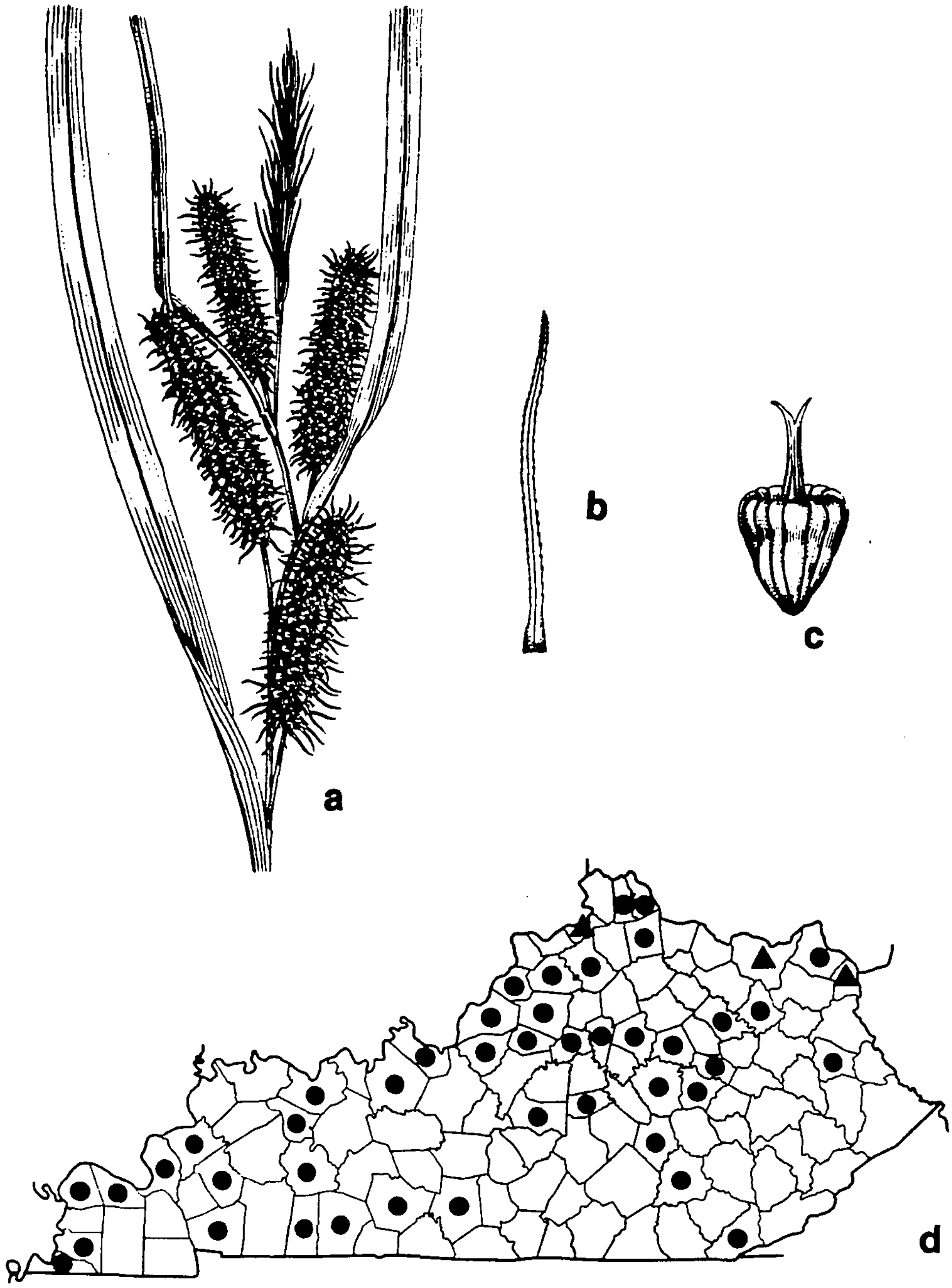

a
b
c
d

Figure 22. CAREX GIGANTEA (a) inflorescence, lower part, X1; (b) inflorescence, upper part, X1; (c) perigynium, X8; (d) distribution map.

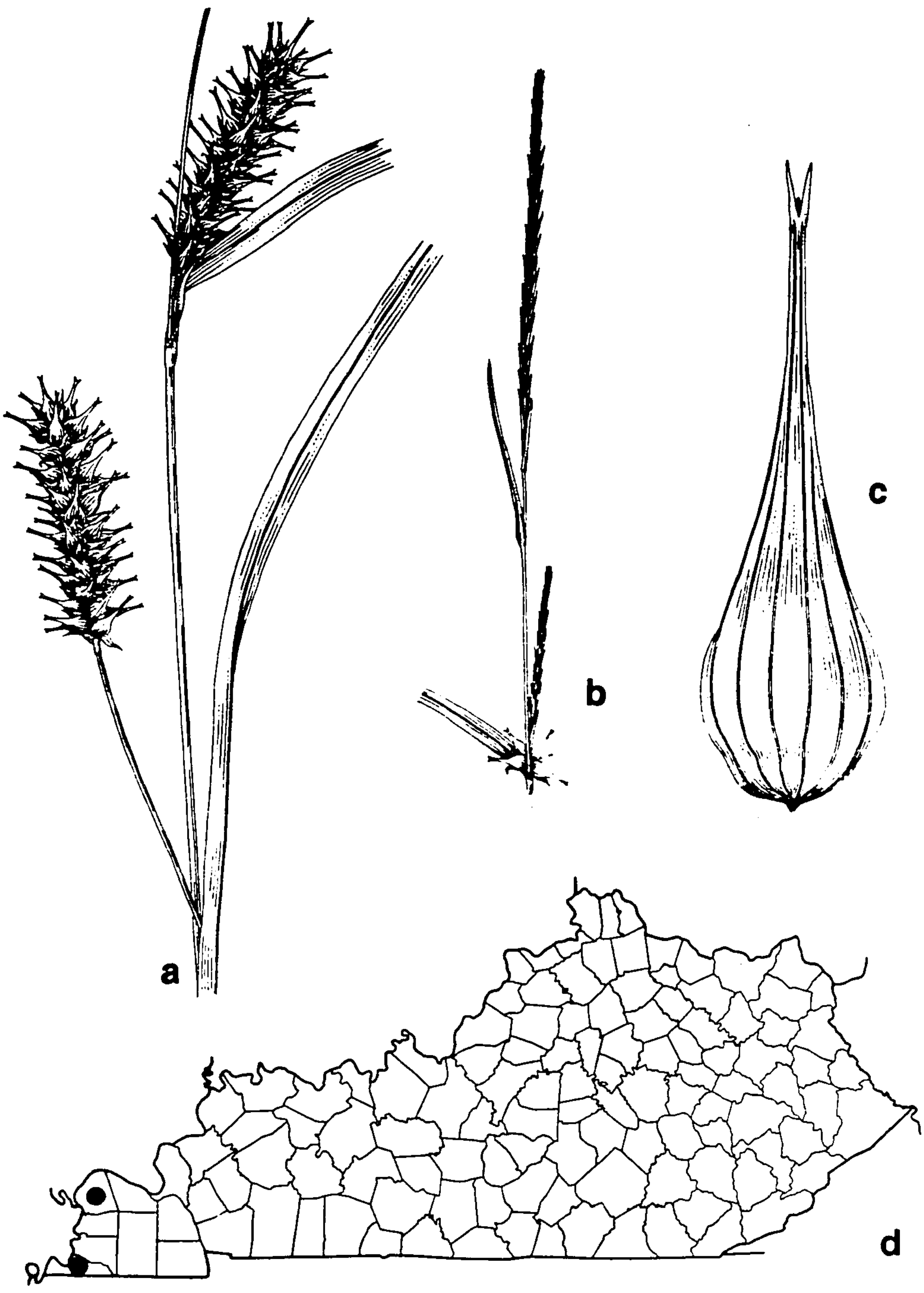

a
b
c
d

Figure 23. CAREX GRACILLIMA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

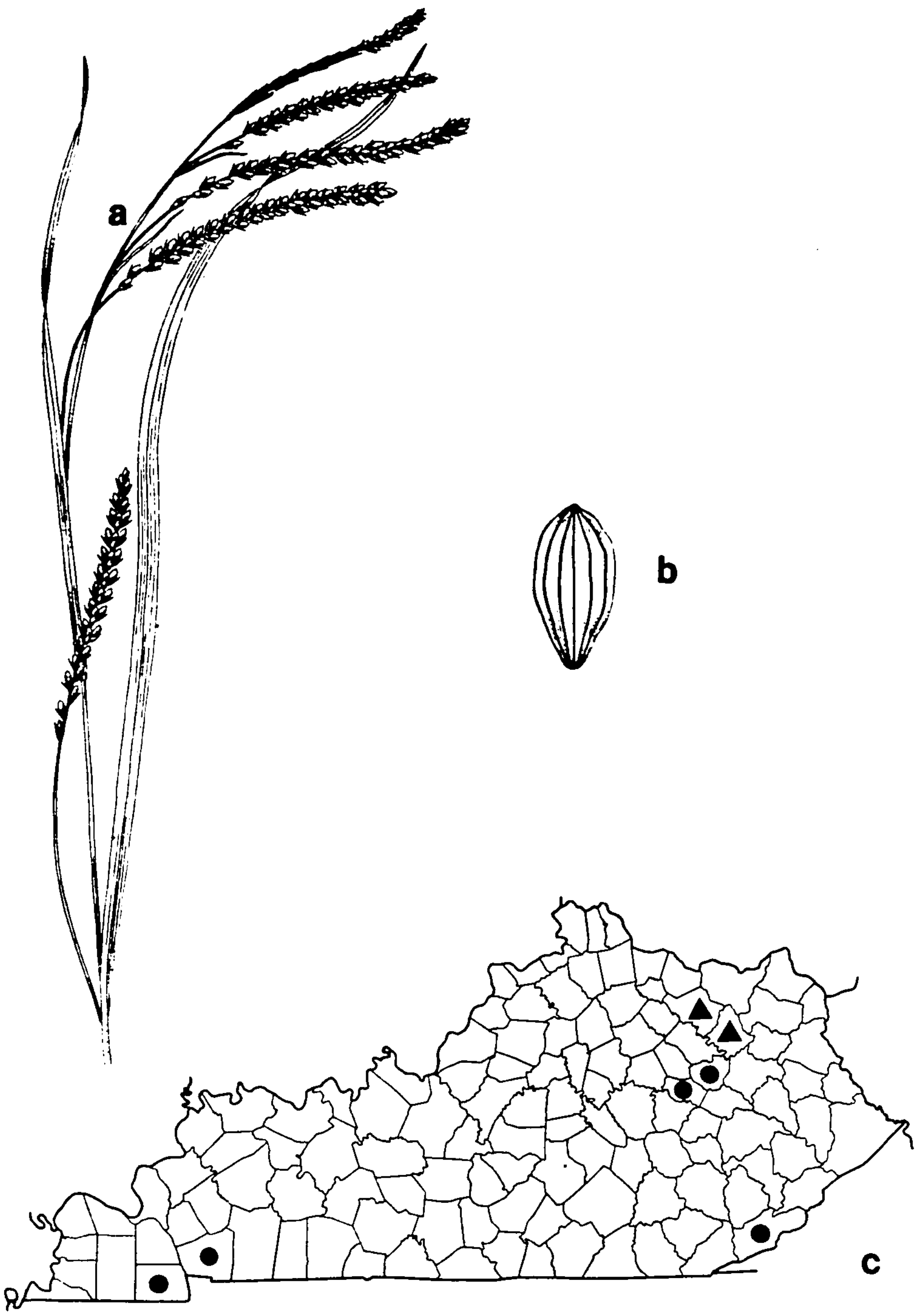

a
b
c

Figure 24. CAREX GRANULARIS (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

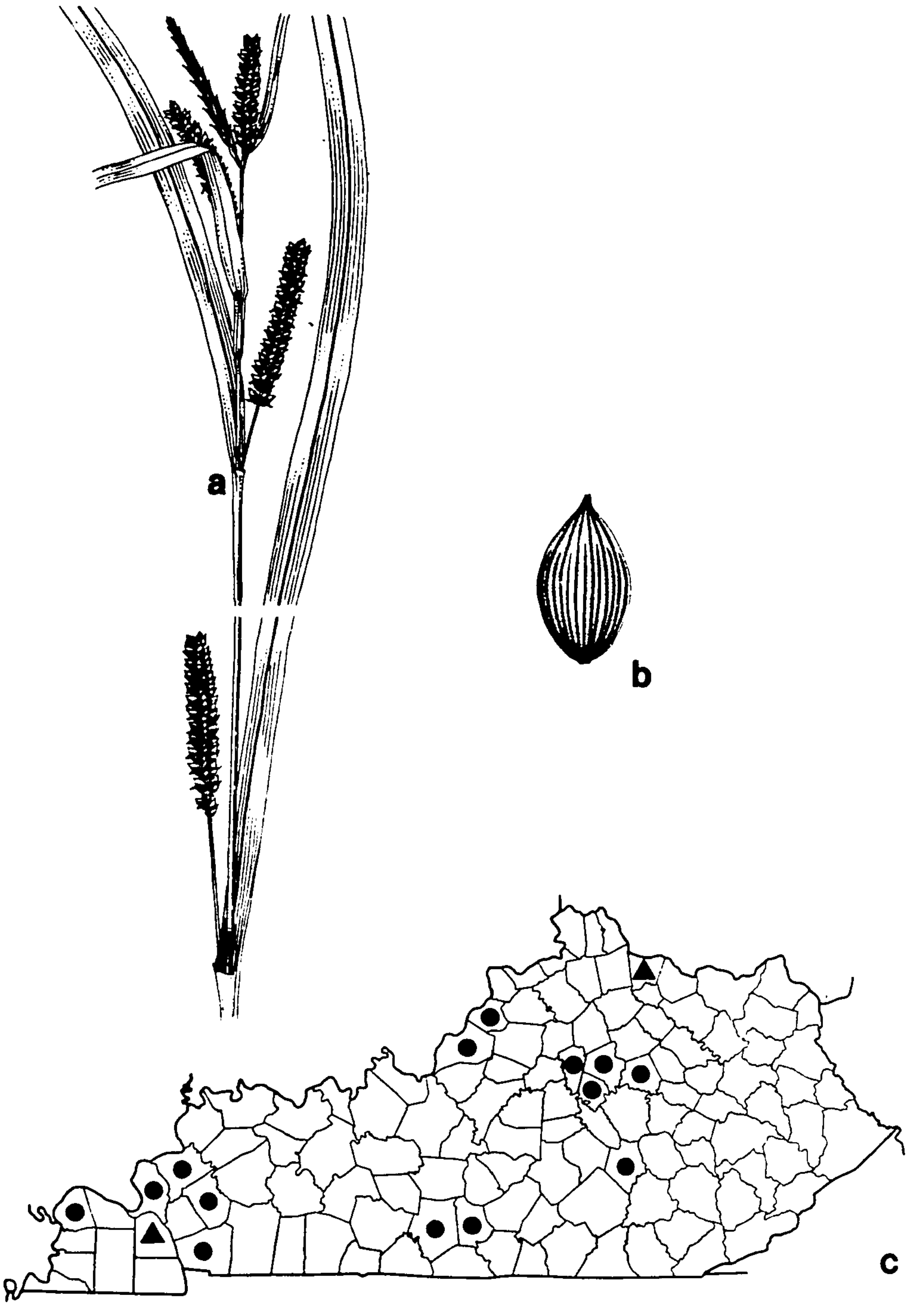

a
b
c

Figure 25. CAREX GRAYI (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

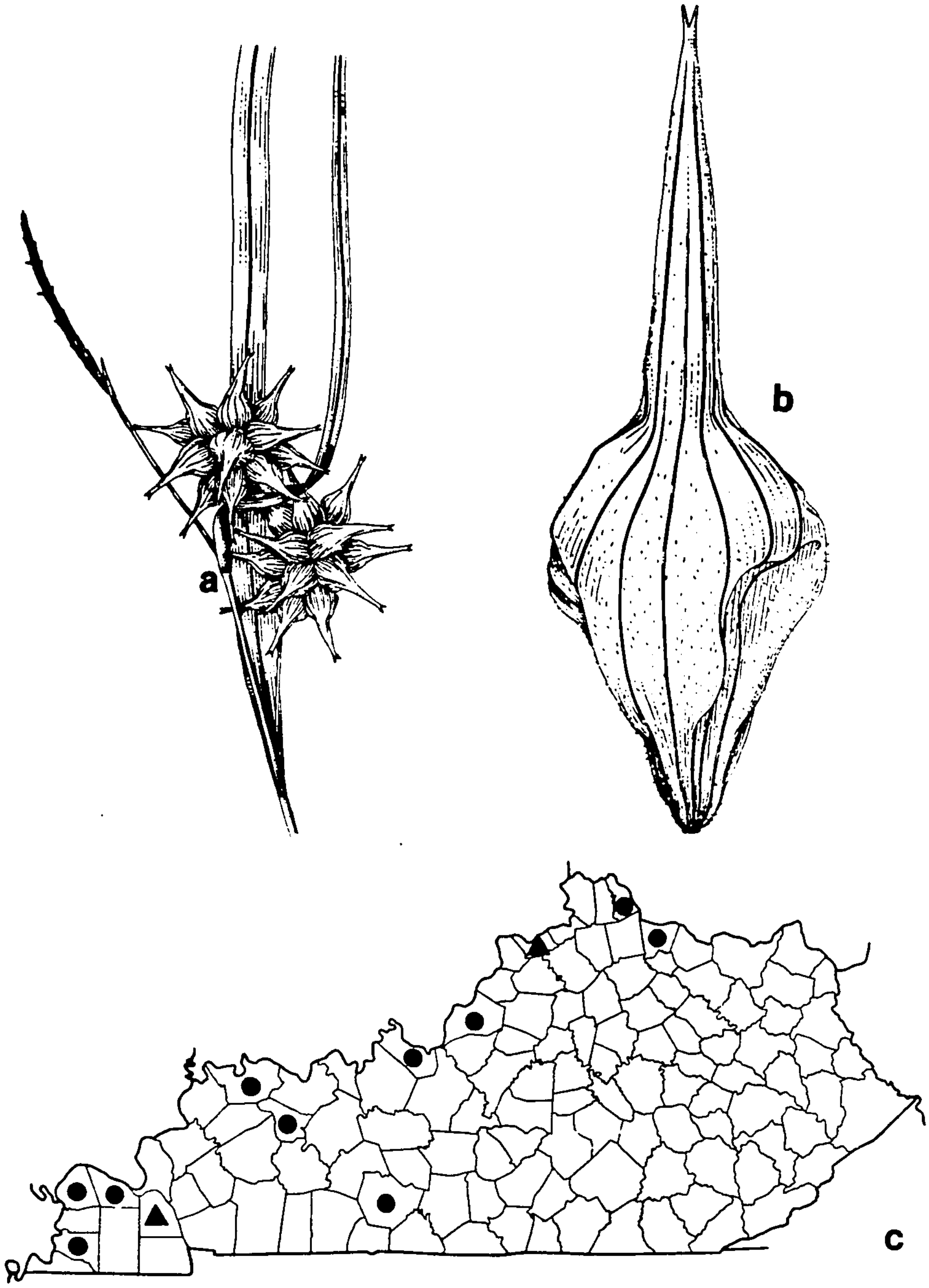
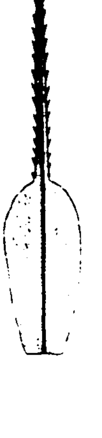
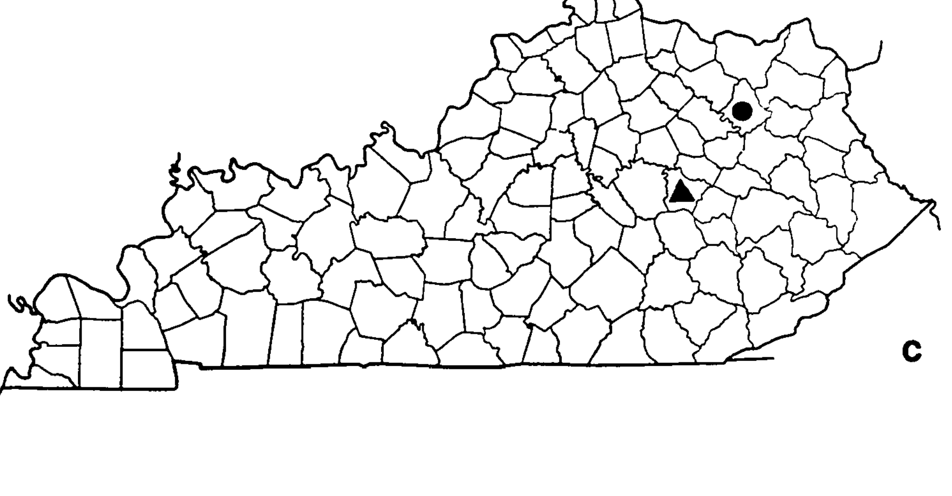

a
b
c

Figure 26. CAREX GYNANDRA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.



a

b



c

Figure 27. CAREX HYSTERICINA (a) inflorescence, X1; (b) perigynium, X8;

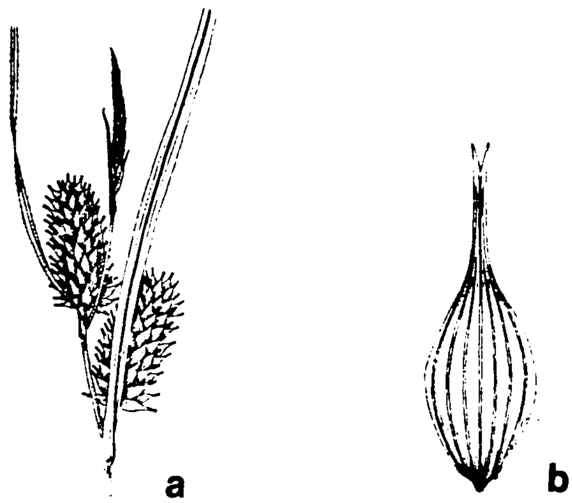

a
b

Figure 28. CAREX INTUMESCENS (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

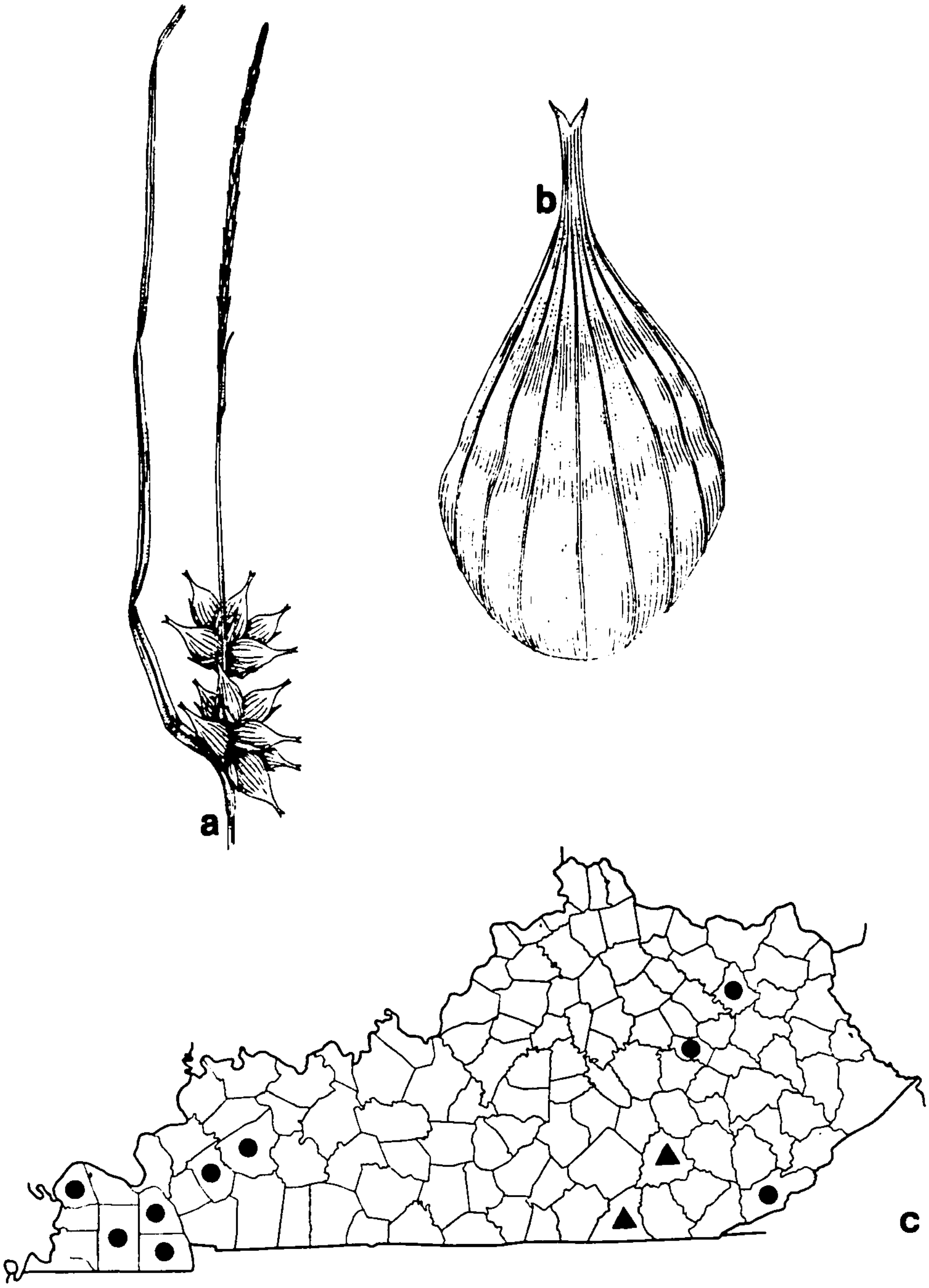

a
b
c

Figure 29. CAREX JOORII (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.


a
b
c

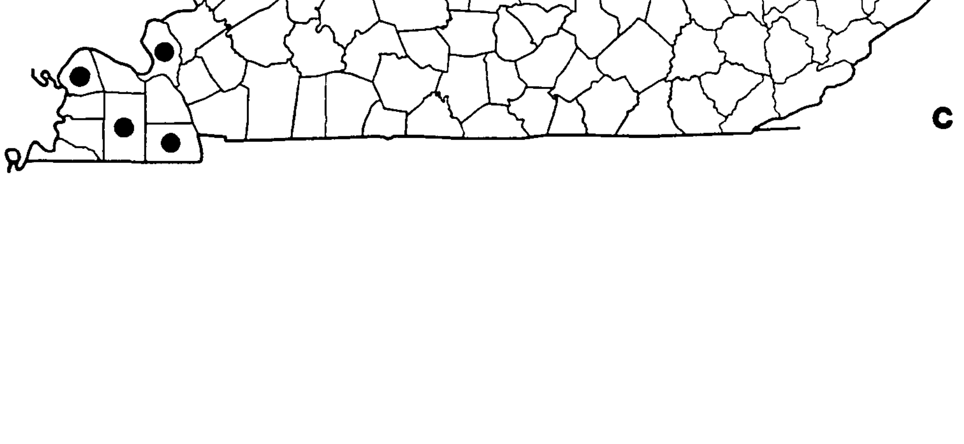
Figure 30. CAREX LACUSTRIS var.LAXIFLORA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.


a
b
c

Figure 31. CAREX LAEVIVAGINATA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

a

b



c

Figure 32. CAREX LANUGINOSA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

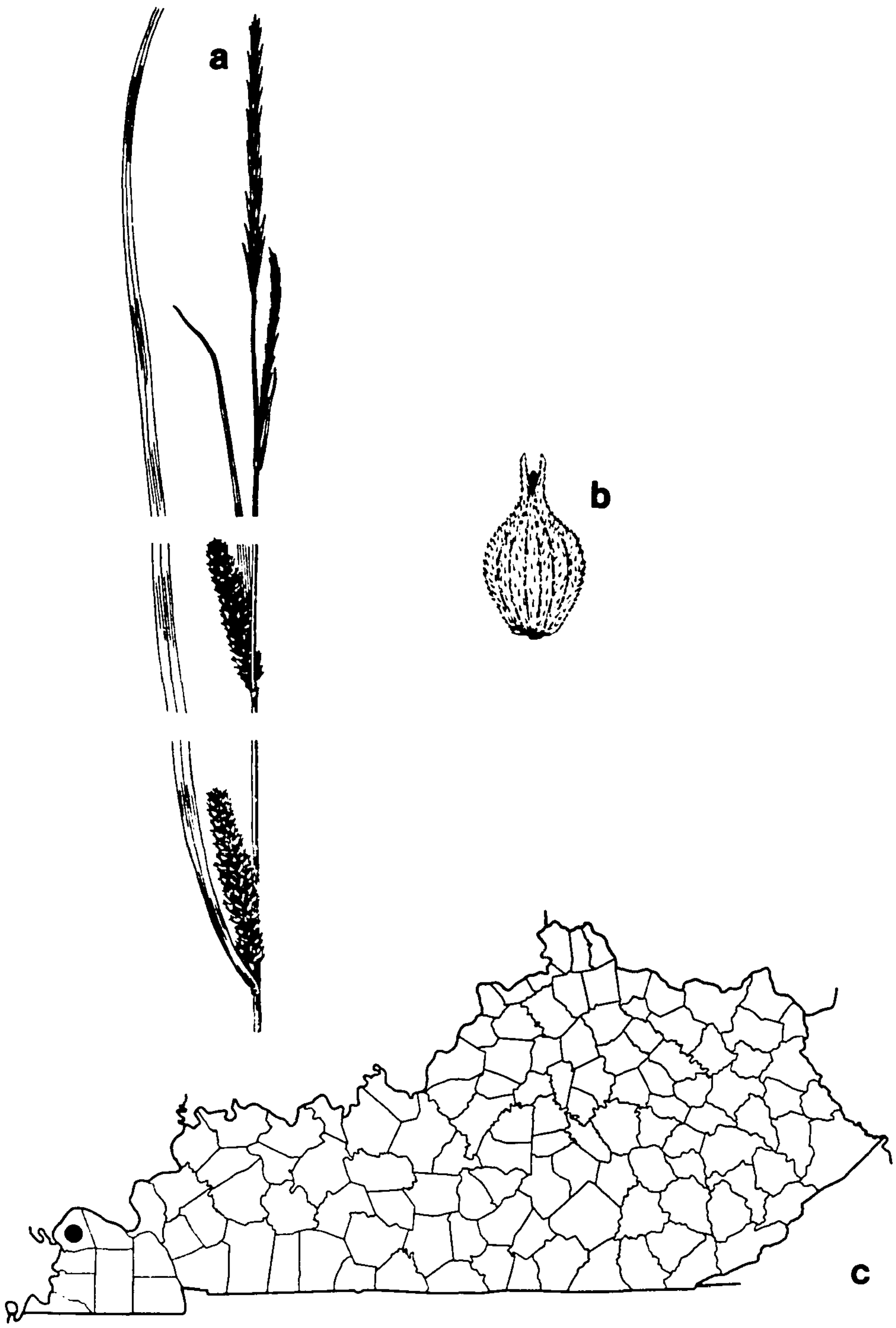
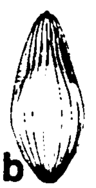
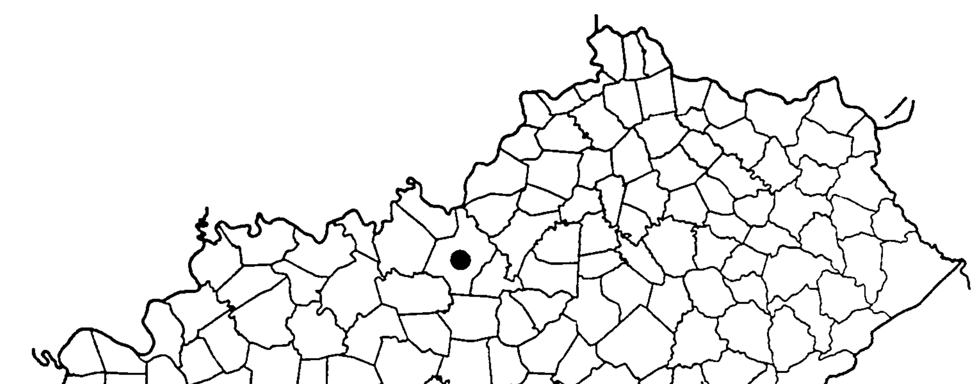

a
b
c

Figure 33. CAREX LEPTALEA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

a



b



c

Figure 34. CAREX LOUISIANICA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

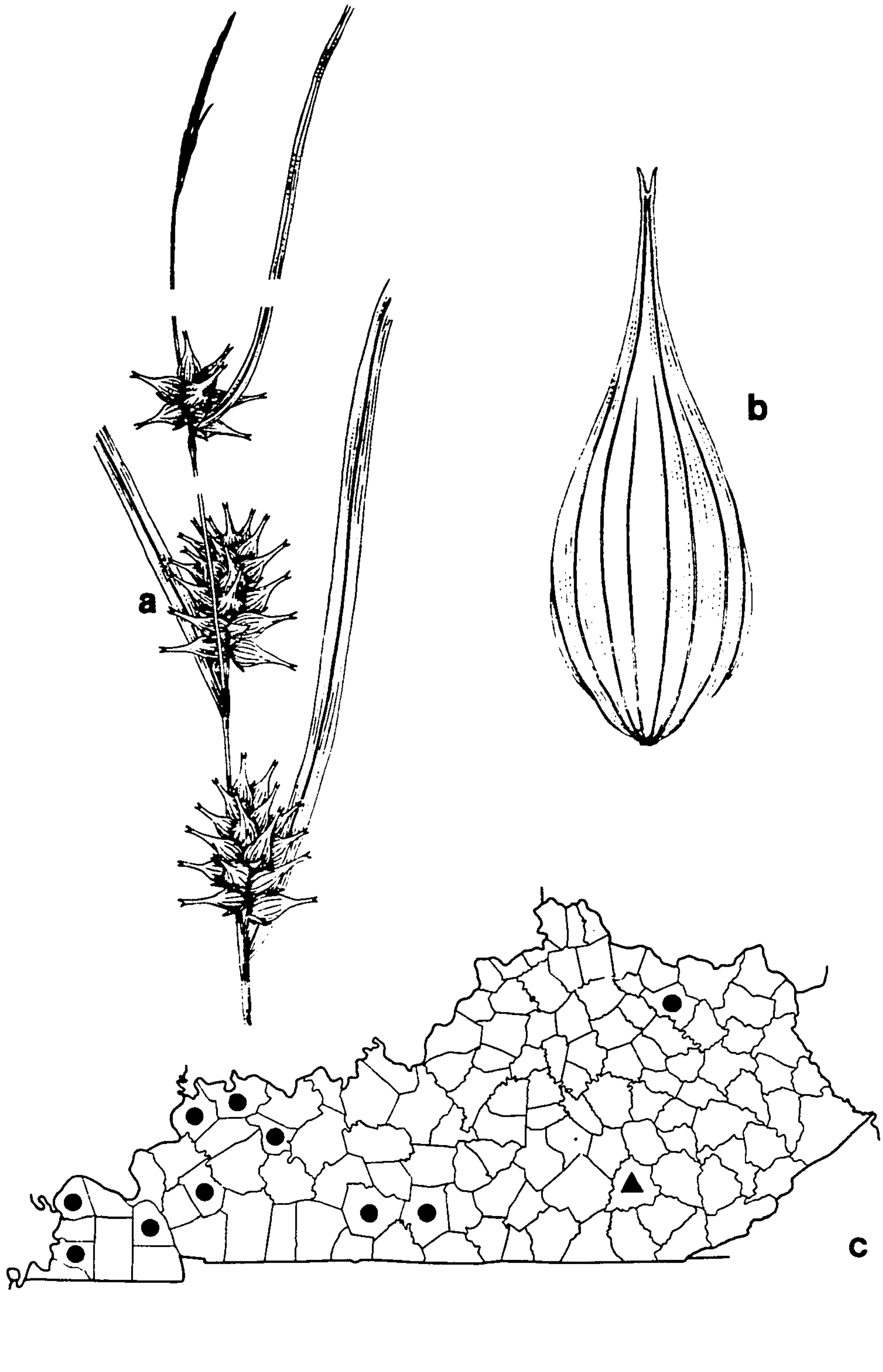

a
b
c

Figure 35. CAREX LUPULINA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

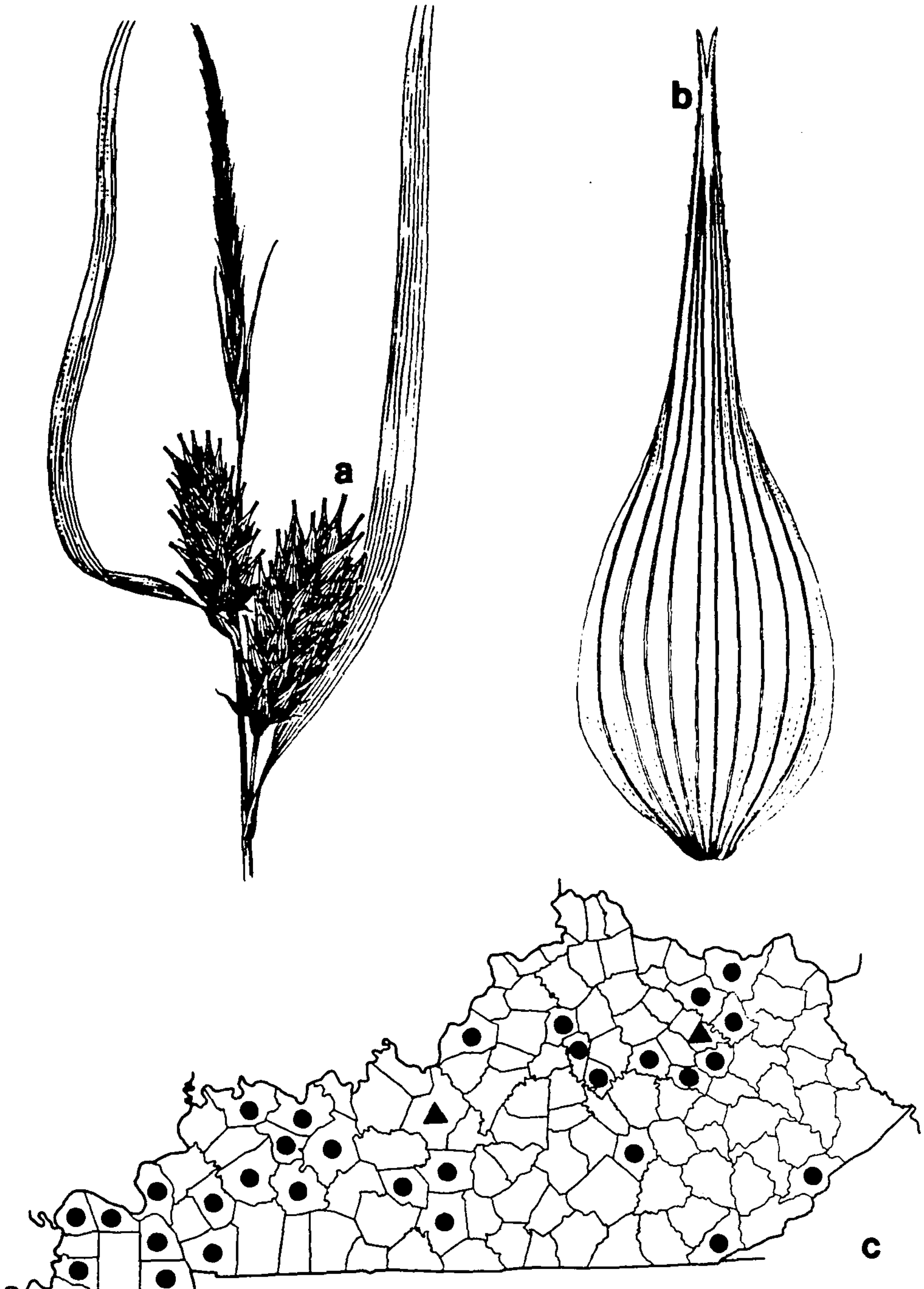

a
b
c

Figure 36. CAREX LURIDA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

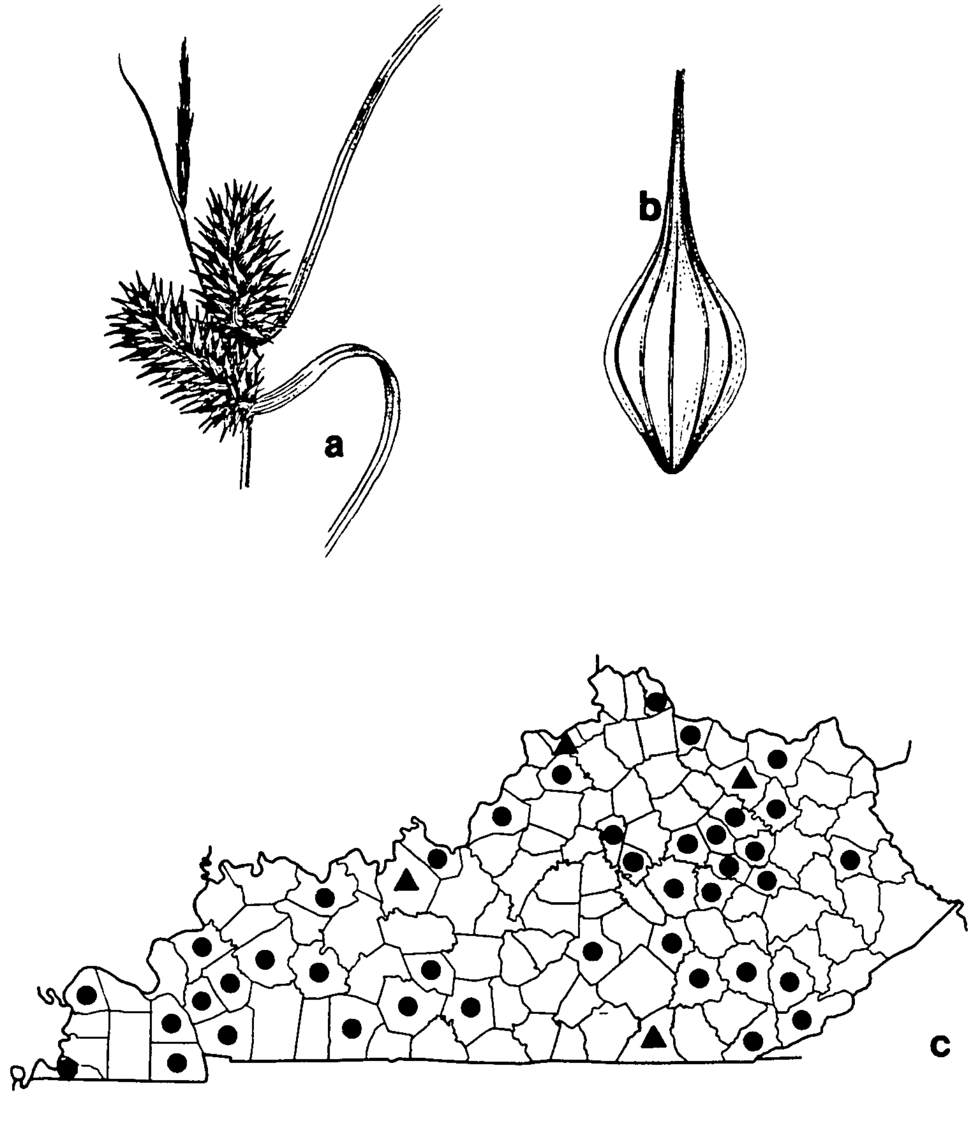

a
b
c

Figure 37. CAREX MUSKINGUMENSIS (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

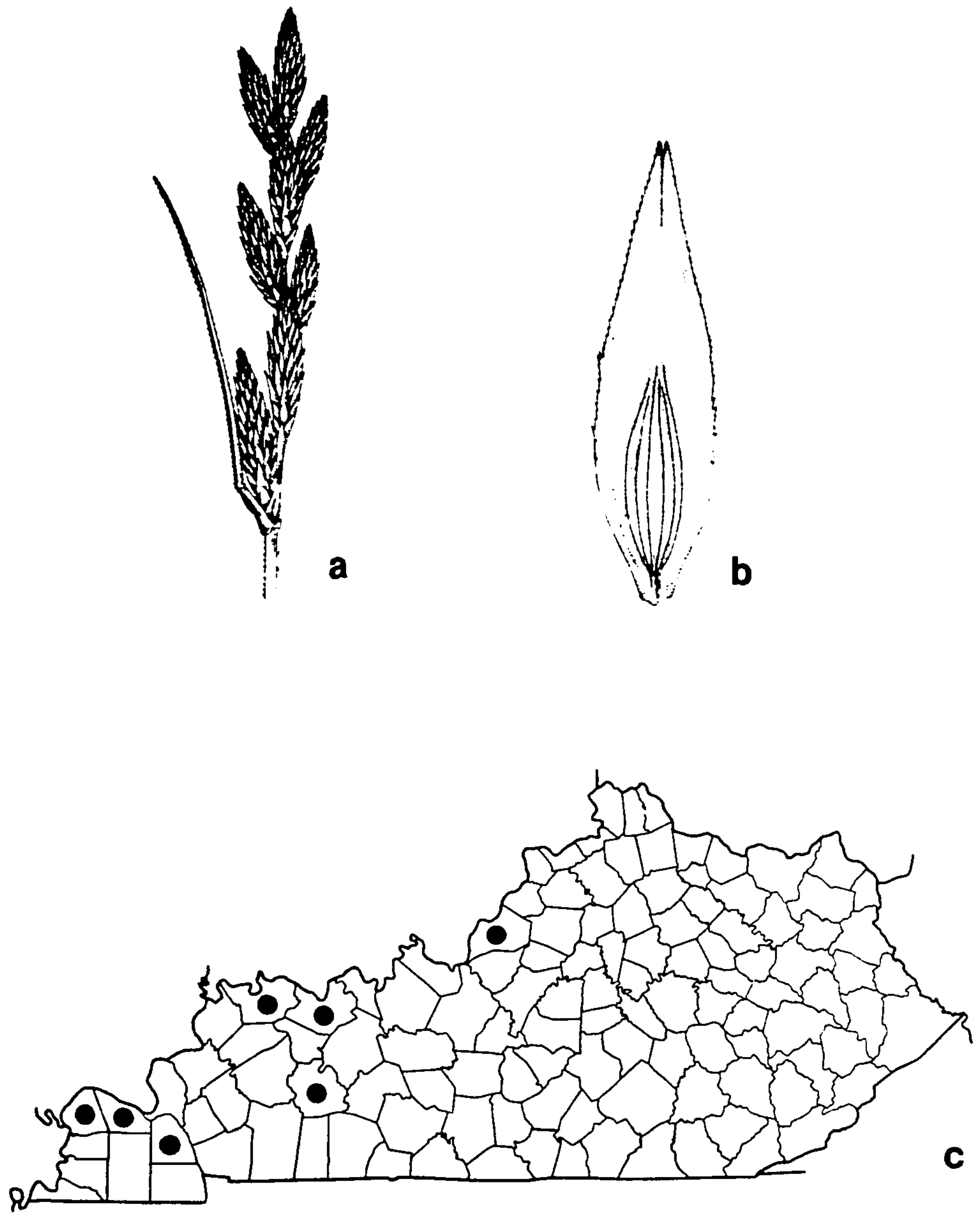

a
b
c

Figure 38. CAREX OXYLEPIS (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.


a
b
c

Figure 39. CAREX PRASINA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

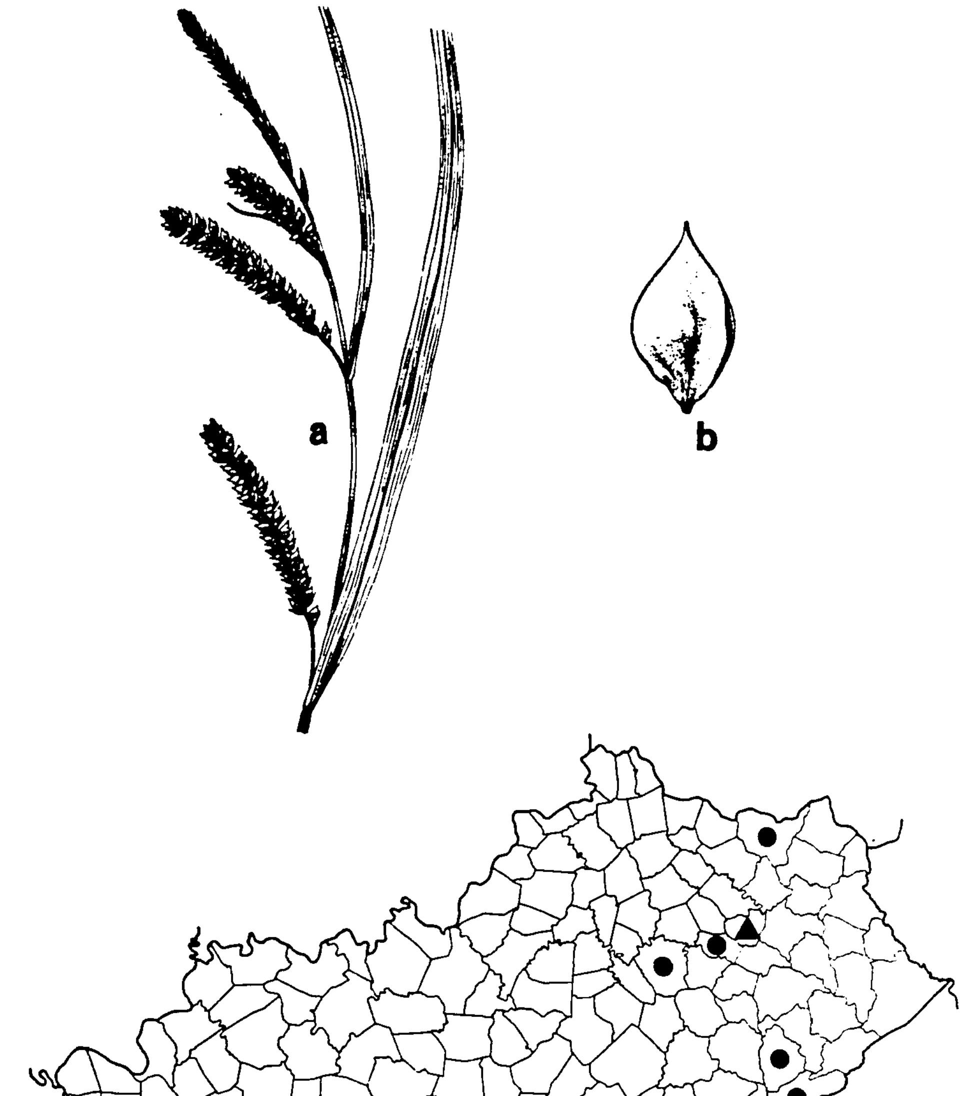

a
b
c

Figure 40. CAREX SCABRATA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

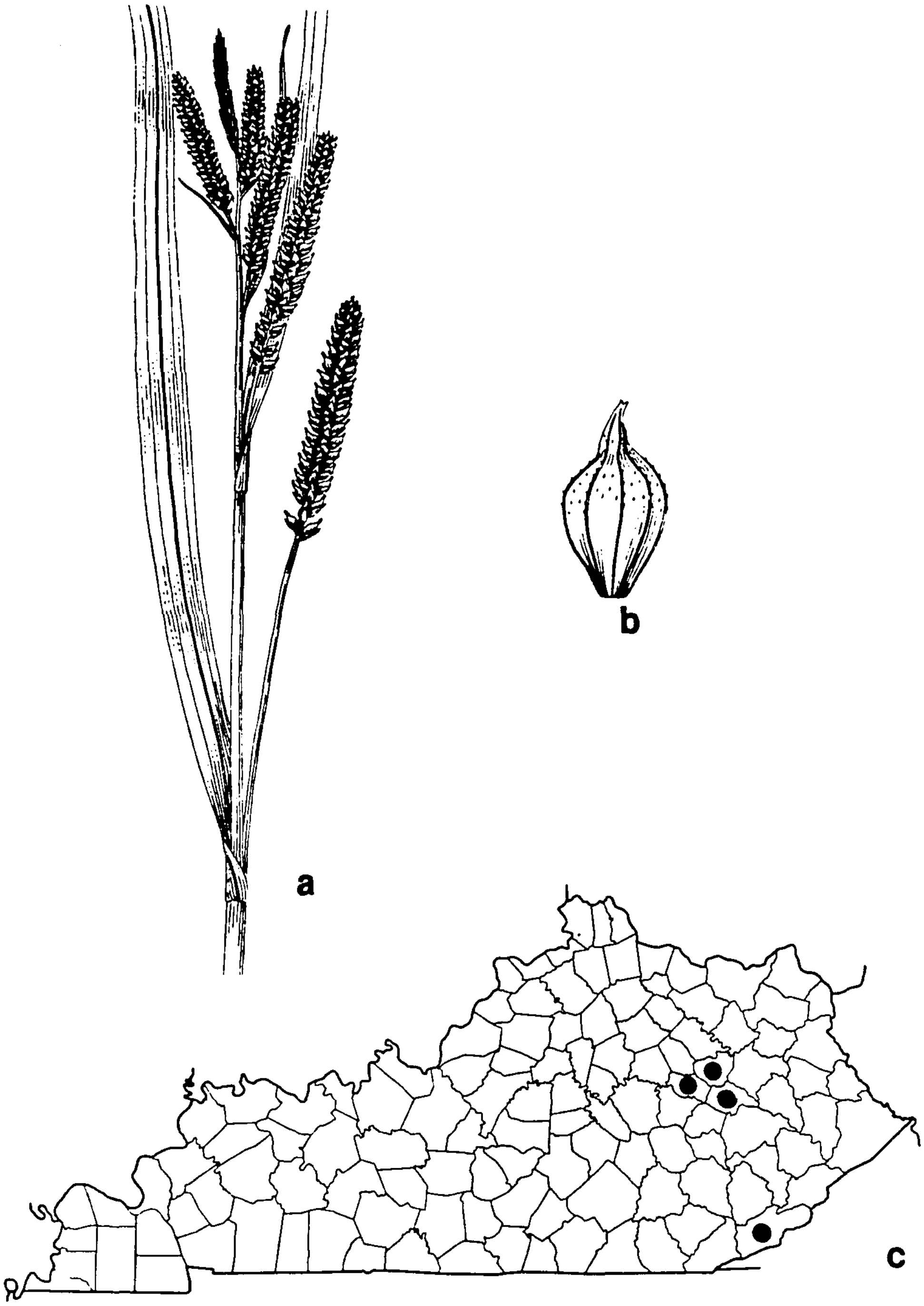
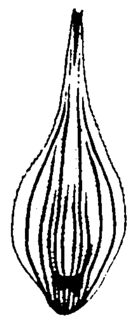
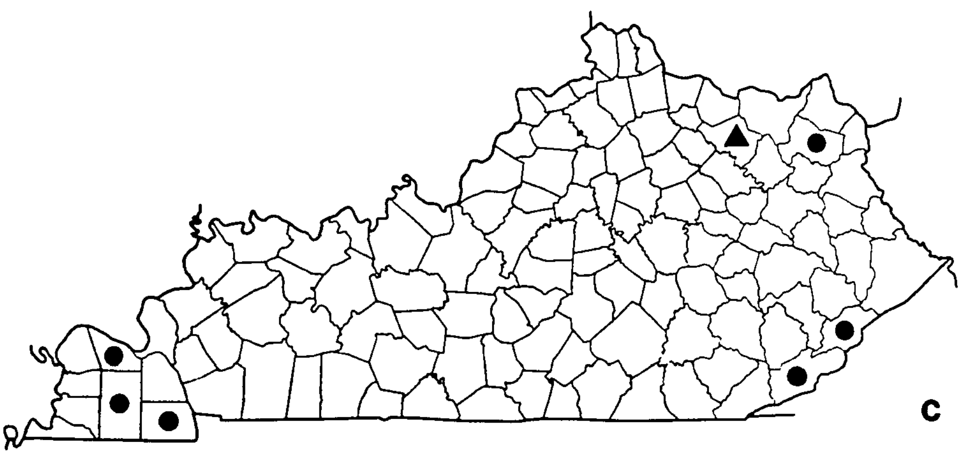

a
b
c

Figure 41. CAREX SCOPARIA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

a



b



c

Figure 42. CAREX SHORTIANA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

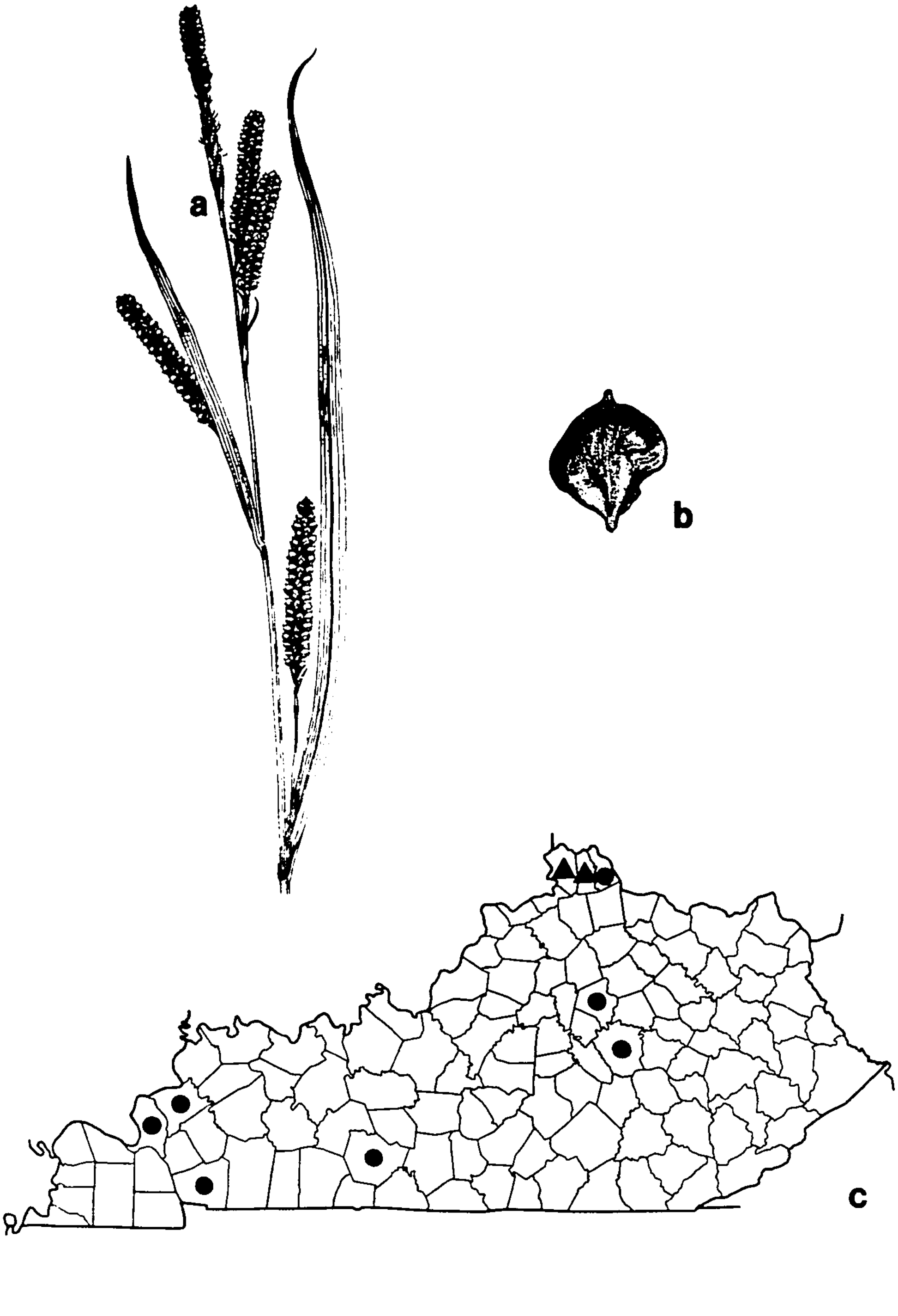
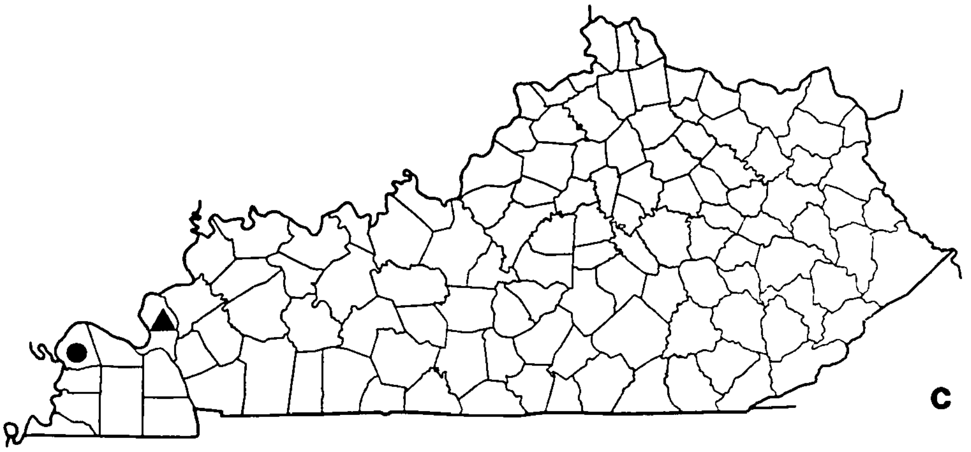

a
b
c

Figure 43. CAREX SOCIALIS (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

a

b



c

Figure 44. CAREX SQUARROSA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

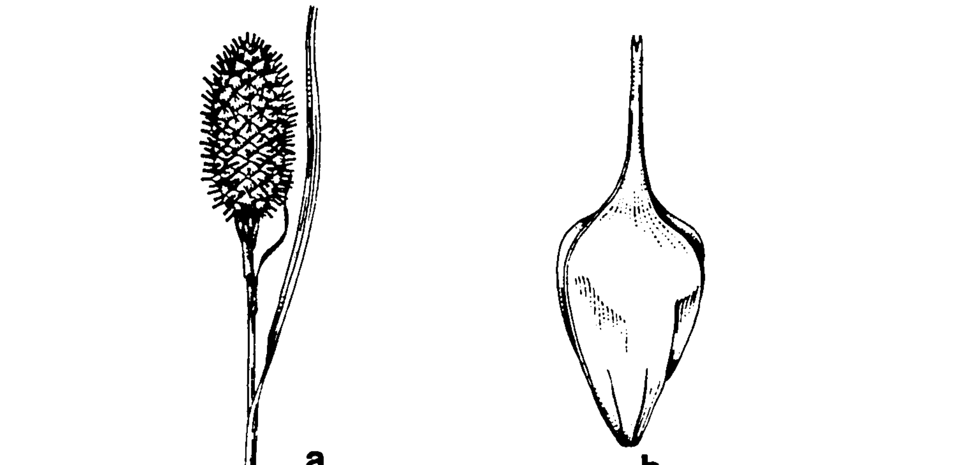

a
b
c

Figure 45. CAREX STIPATA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

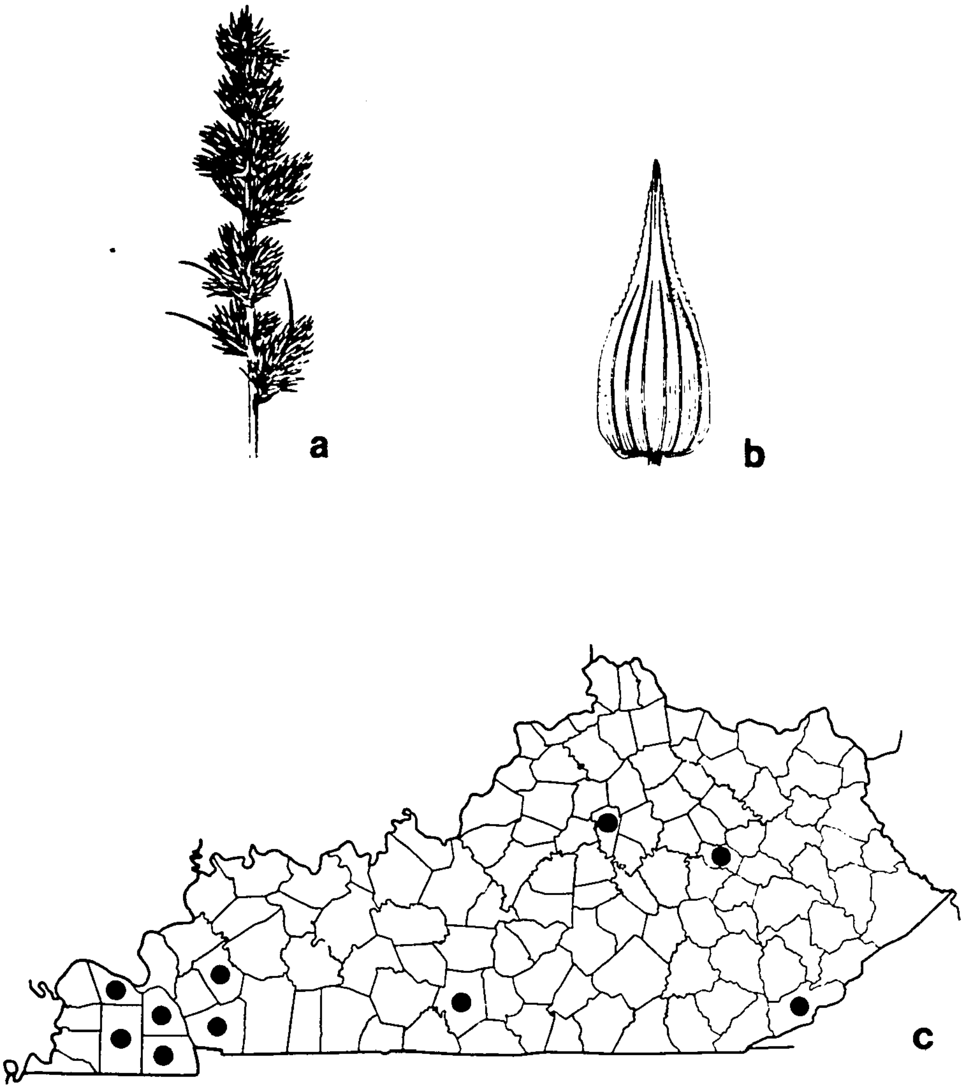

a
b
c

Figure 46. CAREX STRICTA var. STRICTA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

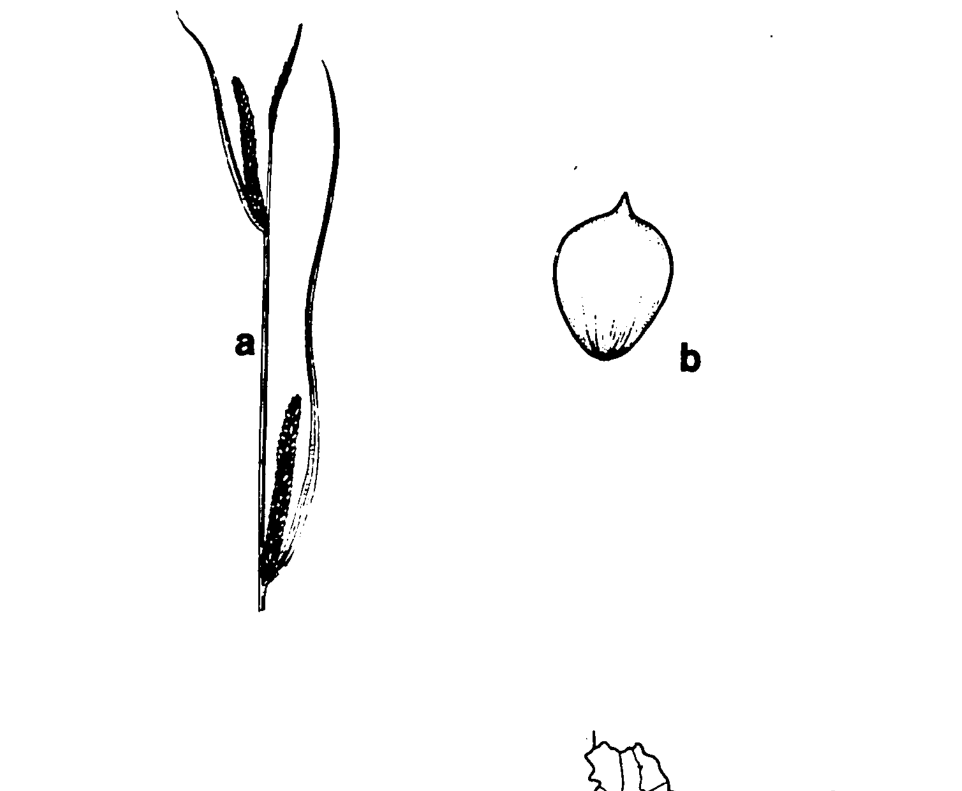

a
b
c

Figure 47. CAREX TORTA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.


a
b
c

Figure 48. CAREX TRIBULOIDES (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

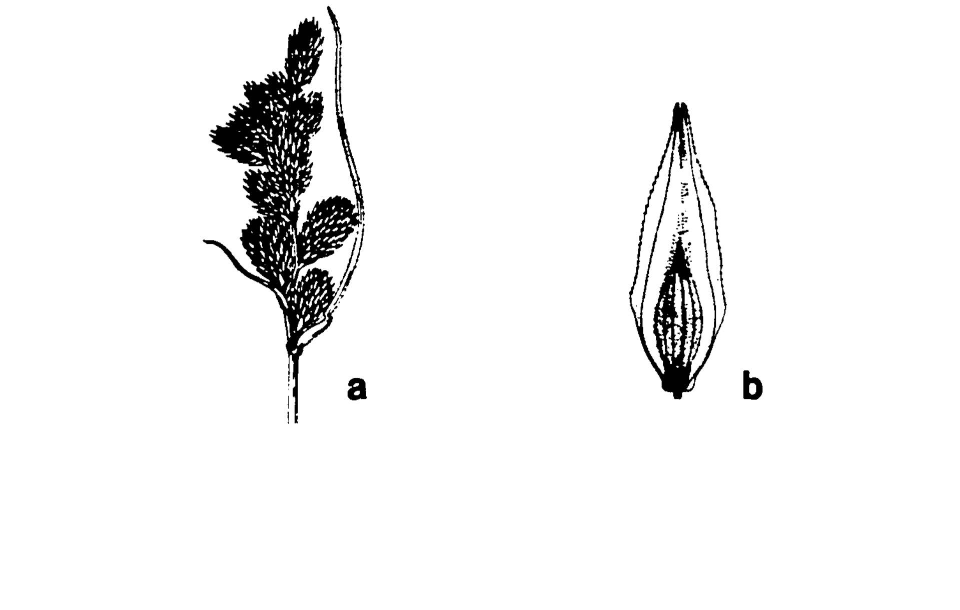

a
b
c

Figure 49. CAREX TYPHINA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

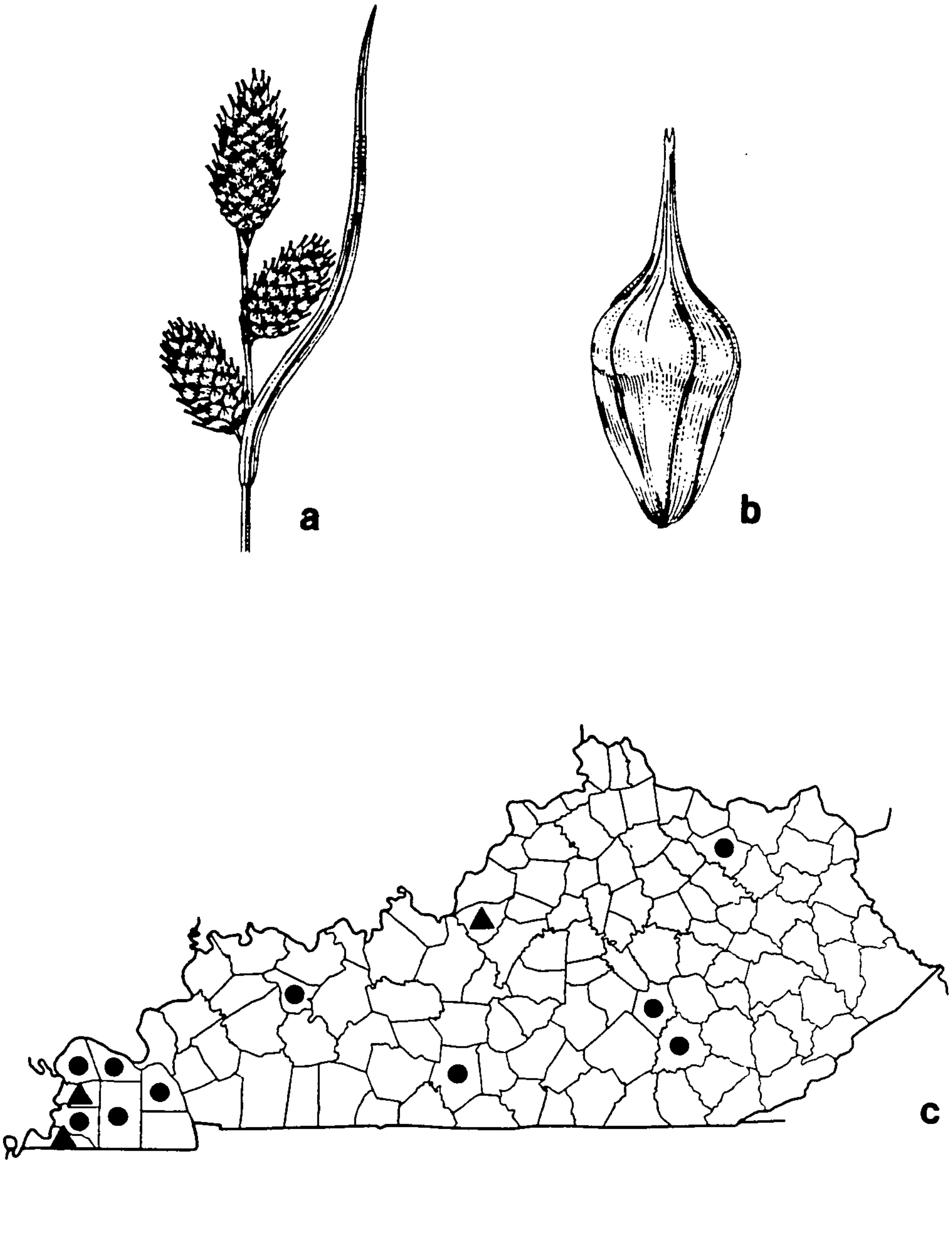

a
b
c

Figure 50. CAREX VESICARIA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.

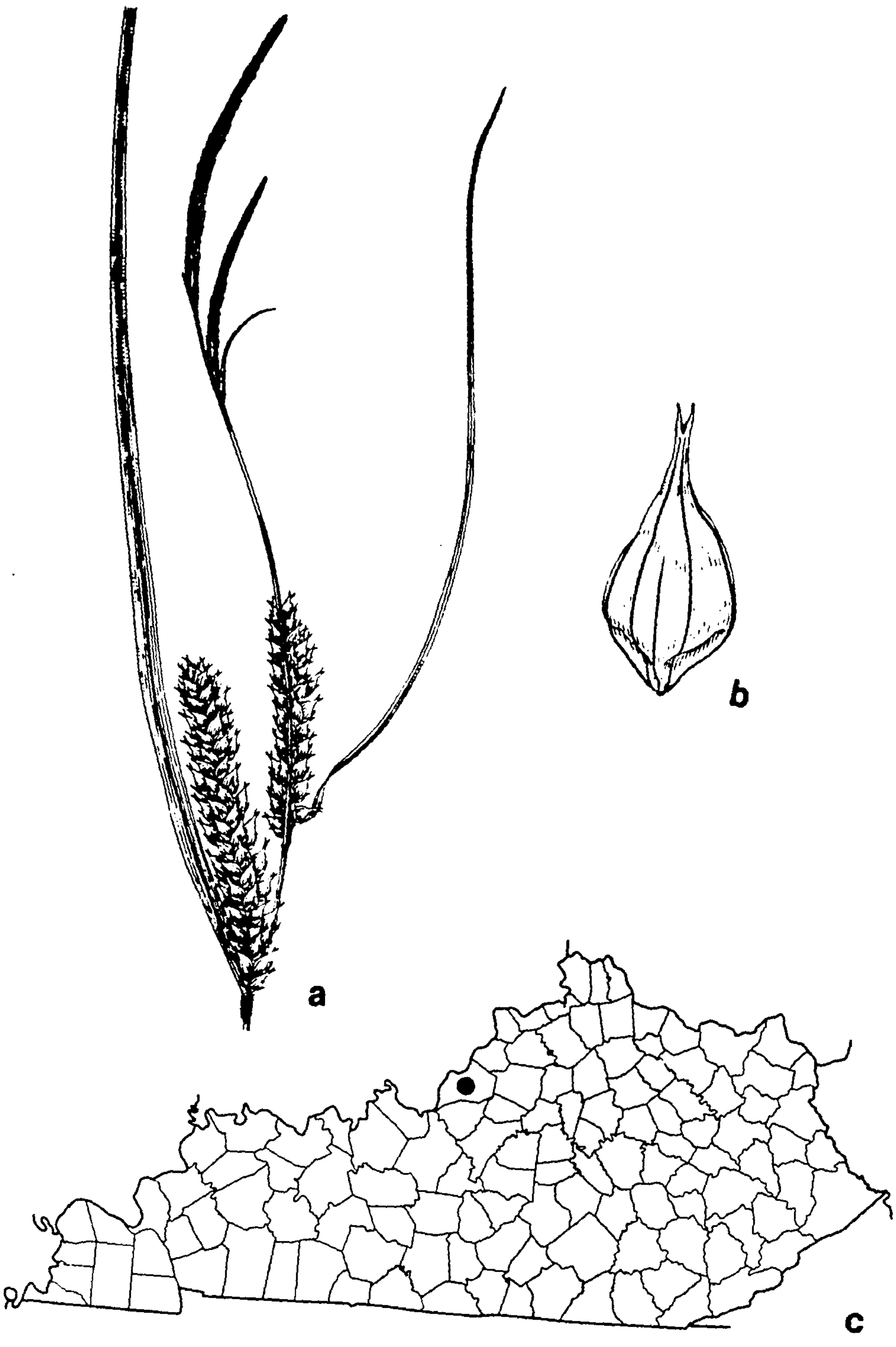

a
b
c

Figure 51. CAREX VULPINOIDEA (a) inflorescence, X1; (b) perigynium, X8; (c) distribution map.


a
b
c