A Revision of Diarrhena (Poaceae) in the United States

David M. Brandenburg; James R. Estes; Scott L. Collins

Bulletin of the Torrey Botanical Club, Vol. 118, No. 2. (Apr. - Jun., 1991), pp. 128-136.

Stable URL:
http://links.jstor.org/sici?sici=0040-9618%28199104%2F06%29118%3A2%3C128%3AAROD%28I%3E2.0.CO%3B2-N

Bulletin of the Torrey Botanical Club is currently published by Torrey Botanical Society.

Bulletin of the Torrey Botanical Club 118(2), 1991, pp. 128–136

A revision of *Diarrhena* (Poaceae) in the United States[1]

David M. Brandenburg, James R. Estes and Scott L. Collins[2]

Oklahoma Biological Survey and Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019

ABSTRACT

BRANDENBURG, D. M., J. R. ESTES, AND S. L. COLLINS (Oklahoma Biological Survey and Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019). A revision of *Diarrhena* (Poaceae) in the United States. Bull. Torrey Bot. Club 118: 128–136. 1991.—Cluster and principal coordinate analyses of *Diarrhena americana* (Poaceae) revealed two non-overlapping groups of OTU's corresponding to *Diarrhena americana* var. *americana* and var. *obovata*. 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, and degree of pericarp-seed coat fusion—occur and are correlated with the two taxa. Consequently, recognition of two species is warranted, and the new combination *Diarrhena obovata* is made.

Key words: *Diarrhena americana, Diarrhena obovata,* Poaceae, cluster analysis, caryopsis.

Diarrhena Beauv. (Poaceae) inhabits woodlands of the central and eastern United States and temperate eastern Asia (Anderson 1958; Koyama and Kawano 1964); however some authors, such as Tsvelev (1983, 1989), treat the Asian species as *Neomolinia* Honda. The subfamilial classification of *Diarrhena* (sensu lato) is also problematic because it combines micro- and macromorphological features of both Pooideae and Bambusoideae (sensu lato) (Tateoka 1957, 1960; McFarlane and Watson 1980; Hilu and Wright 1982; Campbell 1985). Tsvelev (1983, 1989) placed *Diarrhena* and its segregate genus in their own tribe, Diarrheneae of the Pooideae. In contrast, in the most recent monograph of the family, Clayton and Renvoize (1986) tentatively assigned the genus to Bambusoideae, again as an isolated tribe. Currently, *Diarrhena americana* Beauv. is the only recognized species in the United States, although Gleason (1952a, 1952b) described two varieties, *D. americana* var. *americana* and *D. americana* var. *obovata* Gleason. Anderson (1958) concluded that intermediates between the two varieties are widespread and that recognition of the taxa as species is not warranted. However, while preparing a treatment of *Diarrhena* for *Vascular Flora of the Southeastern United States,* we noted consistent morphological differences between the varieties. Thus a reassessment of their taxonomic status seemed justified. We employed scanning electron microscopy and computer-assisted numerical techniques to evaluate the pattern of variation in *D. americana,* specifically to assess the classification of *D. americana* var. *obovata.* For brevity, *D. americana* var. *americana* is herein referred to as AMERICANA and var. *obovata* as OBOVATA, when there is no difficulty in interpretation.

Materials and Methods. Seventy-eight individual herbarium specimens (39 from each variety, sensu Anderson) were selected as operational taxonomic units (OTU's) (Appendix A). To insure adequate sampling, the OTU's were chosen from across the geographic ranges of both varieties. To test Anderson's hypothesis that intermediates unite the two taxa, we selected 37

[1] This study was supported in part by NSF Grant #DEB-8206286 to JRE and DMB. The Oklahoma Biological Survey also provided funds for field work. This manuscript is based on one chapter of a doctoral dissertation submitted to the University of Oklahoma. A complete list of examined specimens and the data matrix may be requested from JRE; please address reprint requests to JRE.

[2] We are especially grateful to Dennis E. Anderson for sharing his ideas and data with us; we regret that he also declined our invitation to serve as a co-author. Dr. Anderson kindly gave his permission to use fig. 4, which was redrawn from his unpublished thesis. We sincerely appreciate R. J. Tyrl, J. J. Skvarla, and J. S. Fletcher for their assistance and for their helpful comments on an earlier draft of this manuscript. We wish to acknowledge G. D. Schnell, D. J. Hough, and W. F. Chissoe for their technical assistance. Finally, we are grateful for loans provided by curators of the herbaria listed herein. Temporary address for JRE: National Science Foundation, 1800 G Street NW, Washington, DC 20550.

Present address for DMB: The Dawes Arboretum, 770 Jacksontown Road S.E., Newark, Ohio 43055

Received for publication February 6, 1990, and in revised form August 16, 1990.

OTU's from regions of sympatry between the two taxa and included possible intermediates (Anderson 1958). In addition to the 78 OTU's measured for numerical analyses, ca. 900 herbarium specimens on loan from ASPC, BHO, BLK, 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 were examined and annotated.

Nineteen morphological characters (Table 1) were measured and coded for each OTU. 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.

We examined features of the caryopses by scanning electron microscopy. Caryopses, selected from herbarium specimens, were mounted whole or were first cross-sectioned with a razor blade and then 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.

The General Similarity Coefficient of GOWER was used to assess phenetic similarity among the OTU's. We used GOWER (Hough 1981) to produce an OTU by OTU similarity matrix based upon the 19 morphological characters. The GOWER coefficient 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 the relationship between the dendrogram and the original similarity matrix.

We subjected the OTU similarity matrix to principal coordinate analysis to assess continuous variation. Because character loadings cannot 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 coordinate analysis. Thus, the relative position of each OTU along each of the first three axes could be associated with those characters that contributed most to the ordination.

Table 1. Characters of *Diarrhena americana* selected for analysis. Coding of unordered, multistate characters listed in parentheses. * = characters used in discriminant functions analysis.

1. Vestiture of lowermost sheath (0 = glabrous; 1 = pubescent).
2. Vestiture of uppermost sheath (0 = glabrous; 1 = pubescent).
*3. Vestiture of adaxial surface of blades (0 = glabrous; 1 = pubescent).
4. Vestiture of callus of lemma (except first floret) (0 = glabrous; 1 = pubescent).
*5. Shape of lemma (0 = obovate; 1 = elliptic; 2 = lanceolate).
*6. Length of shortest first glume.
*7. Length of longest first glume.
*8. Length of shortest second glume.
*9. Length of longest second glume.
*10. Length of shortest first lemma.
*11. Length of 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 (0 = no hairs ≥ 0.5 mm long; 1 = at least some hairs ≥ 0.5 mm long).
*17. Length/width ratio of second glume.
*18. Length/width ratio of lemma.
19. Shape of beak on caryopsis (0 = blunt and broad; 1 = bottlenosed).

UPGMA and principal coordinate analysis were executed with the numerical taxonomy system programs (NT-SYS; Rohlf *et al.* 1979).

Stepwise discriminant functions analysis was used to assess the efficacy of the cluster analysis and to identify the morphological characters that best define the groups that were identified by cluster analysis. Because the discriminant functions program (BMDP-P7M; Dixon 1983) is incapable of handling missing data, characters with missing values were deleted from the analysis. Binary characters with little or no within-group variance (e.g., callus pubescence) were deleted also. Thus, only 11 of the original 19 characters were used in this analysis (Table 1).

Results and Discussion. Our 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 (Brandenburg 1985). 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 original resemblance matrix. The same groups ap-

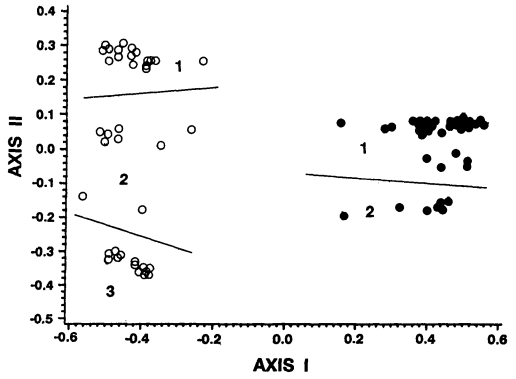

Fig. 1. OTU's of North American *Diarrhena* plotted with respect to the first two axes of principal coordinate analysis. Symbols: ● = AMERICANA; ○ = OBOVATA. Subclusters: AMERICANA: 1 = all sheaths pubescent; 2 = lower sheaths glabrous, upper sheaths pubescent. OBOVATA: 1 = pubescent blades and pubescent sheaths; 2 = pubescent blades, but upper and/or lower sheaths glabrous; 3 = glabrous blades and sheaths.

peared in the plot of the first two axes of principal coordinate analysis (Fig. 1). Axis I accounted for 51.5% of the variance; it was correlated ($P < 0.001$) with 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. Vestiture of blades and sheaths was significantly correlated with axis II, which accounted for 11% of the variance, ($P < 0.001$). The two clusters are separated into subclusters on axis II. In the AMERICANA group, subcluster 1 consists of individuals with all sheaths pubescent, whereas subcluster 2 includes specimens with glabrous lower sheaths and pubescent upper sheaths. The OBOVATA cluster is subclustered on the basis of vestiture of sheaths and of adaxial surface of blades. The numbered subclusters in Fig. 1 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. 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 coordinate and cluster analyses were unambiguously separated by a combination of four characters. The results of the analysis are even more significant because three characters for which there is very little or no overlap between the two taxa—caryopsis type, callus vestiture, and axis vestiture—were not used in the discriminant analysis. Of the characters utilized, the length of

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

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 other is unequivocal.

In our study of the 78 OTU's, we realized that there are two distinct caryopsis types, differing in size (Table 3), shape of the body (Fig. 2a, b), shape of the beak (Fig. 2c, d), and degree of pericarp-seed coat fusion (Fig. 2e, f). Caryopses of OBOVATA have a bottlenose-shaped beak with the body abruptly widened below (Fig. 2b, d). In contrast, caryopses of AMERICANA have a broad, blunt beak that tapers gently into a narrower body (Fig. 2a, c). In addition, the pericarp of AMERICANA is mostly fused to the seed coat (Fig. 2e), whereas that of OBOVATA is mostly free from the seed coat (Fig. 2f). Examination of caropses from plants not used as OTU's confirmed the occurrence of these two distinct types without intermediates. Beak shape is a reflection of expression of development of the upper portion of the ovary (Tateoka 1960; Schwab 1971). Therefore, the shape is apparent early in development, and the two types of caryopses 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 ours indicates 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 thick, opaque pericarp over most of the body of the caryopsis. The pericarp is mostly thin and transparent in the other species, being thick only in scattered areas.

Diarrhena americana is confined to the United States, and the two entities are sympatric in some areas (Fig. 3). OBOVATA occurs predominantly in the prairie states, whereas AMERICANA oc-

Table 3. Diagnostic features of the North American species of *Diarrhena*.

Character	AMERICANA	OBOVATA
1. Vestiture of lemma callus (except first floret)	pubescent	glabrous
2. Vestiture of inflorescence axis	scabrous, some hairs ≥ 0.5 mm	scabrous
3. Beak of caryopsis	broad and blunt	bottlenosed
4. Shape of lemma	lanceolate	obovate or elliptic
5. Apex of lemma	gently tapering to cusp	abruptly tapering to cusp
6. Shortest first lemma	7.1–9.5 mm	4.6–6.6 mm
7. Width of mature caryopsis	1.3–1.8 mm	1.8–2.5 mm

curs southeast of this region with disjunct populations in the Ouachita and Ozark mountains. Both taxa are found in similar woodland habitats, and no phenological differences were detected from information on herbarium labels. No differences in the perceived morphological patterns in areas of sympatry were observed.

Gleason (1952b) recognized two varieties of *Diarrhena americana* based on indumentum of the panicle axes, length of the first and second glumes, and shape, apex, and length of the lemmas. However, we found overlap in the range of variation of each character that he used to circumscribe the two varieties. Therefore, none of the characters which he used consistently discriminate the two taxa. 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 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 he considered insufficient to warrant recognition of the two entities as species. Surprisingly, Gleason (1952b) failed to mention the presence or absence of callus hairs.

The results of our 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 3). We suggest that previous studies of these taxa reported intermediates between them only because the characters chosen to circumscribe the two were inadequate. We found no overlap for caryopsis type, and overlap was slight or nonexistent for several other characters (Table 3). Therefore, we recognize two species of *Diarrhena* in North America. Because no previous specific epithet exists for *D. americana* var. *obovata,* the appropriate new combination is made herein.

There is no direct evidence concerning the origin of either of these two species. However, the grassland biome is more recently derived than the eastern deciduous forest, and replaced the latter vegetation type after the middle Miocene (Axelrod 1985). Also, *Diarrhena americana* var. *americana* is phenetically more similar to the Asian congeners. These patterns provide circumstantial evidence that the prairie taxon, *D. obovata,* is derived from its more southern and eastern counterpart.

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 inconspicuous, typically eccentric; apex long tapering; base tapering. *Inflorescence* a narrow panicle, racemose at apex, long exserted and arching; primary branches ascend-

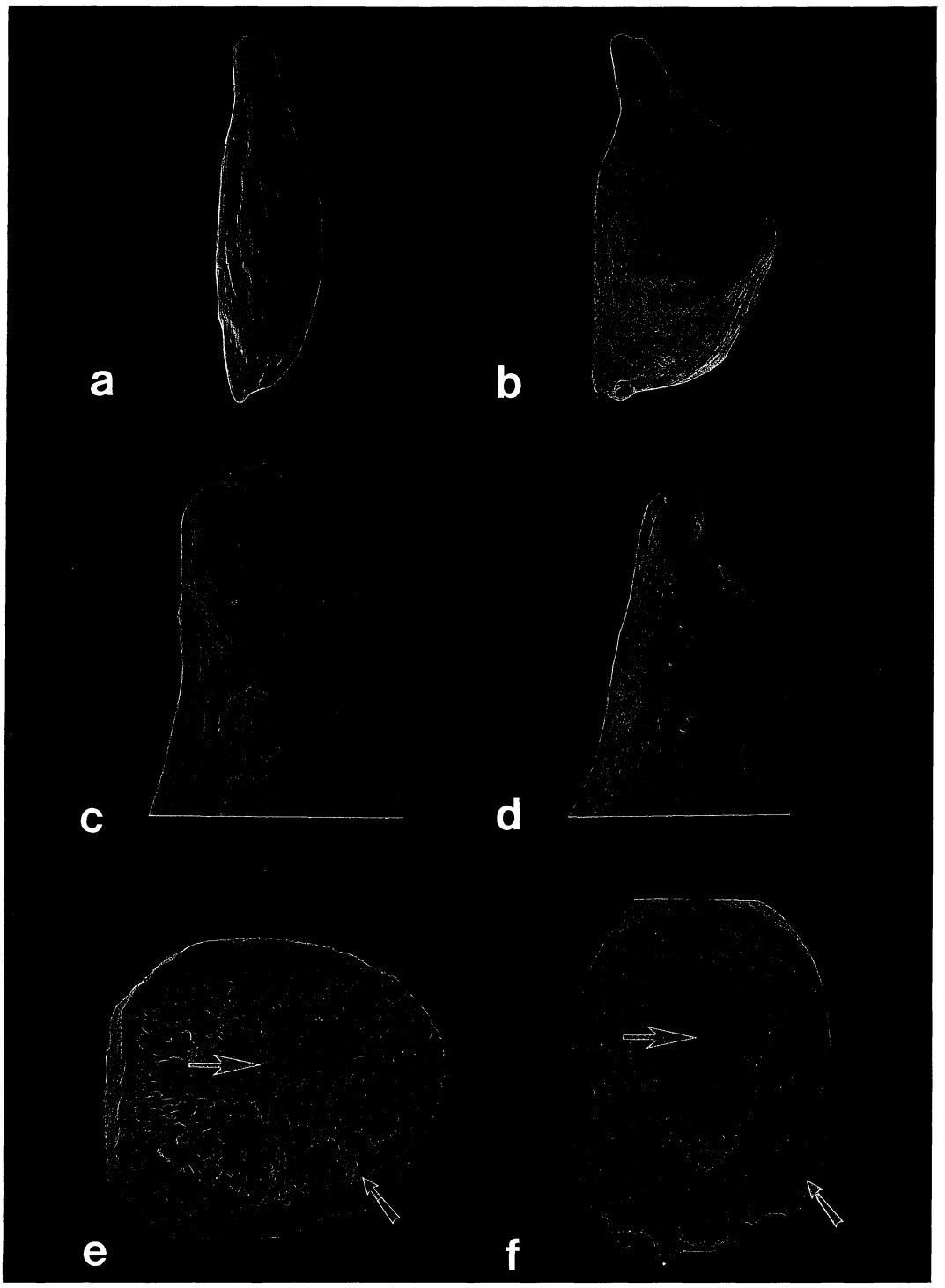

Fig. 2. Caryopses of North American *Diarrhena*. AMERICANA (*Ahles, 6955*: ILL): (a) whole caryopsis (×8.5); (c) beak (×45); (e) cross-section (×35), lower arrow = fusion of pericarp and seed coat, upper arrow = endosperm solid in center. OBOVATA (*Anderson, 1072*: ISC): (b) whole caryopsis (×8.5); (d) beak (×45); (f) cross-section (×30), lower arrow = pericarp free from seed coat, upper arrow = central cavity in endosperm.

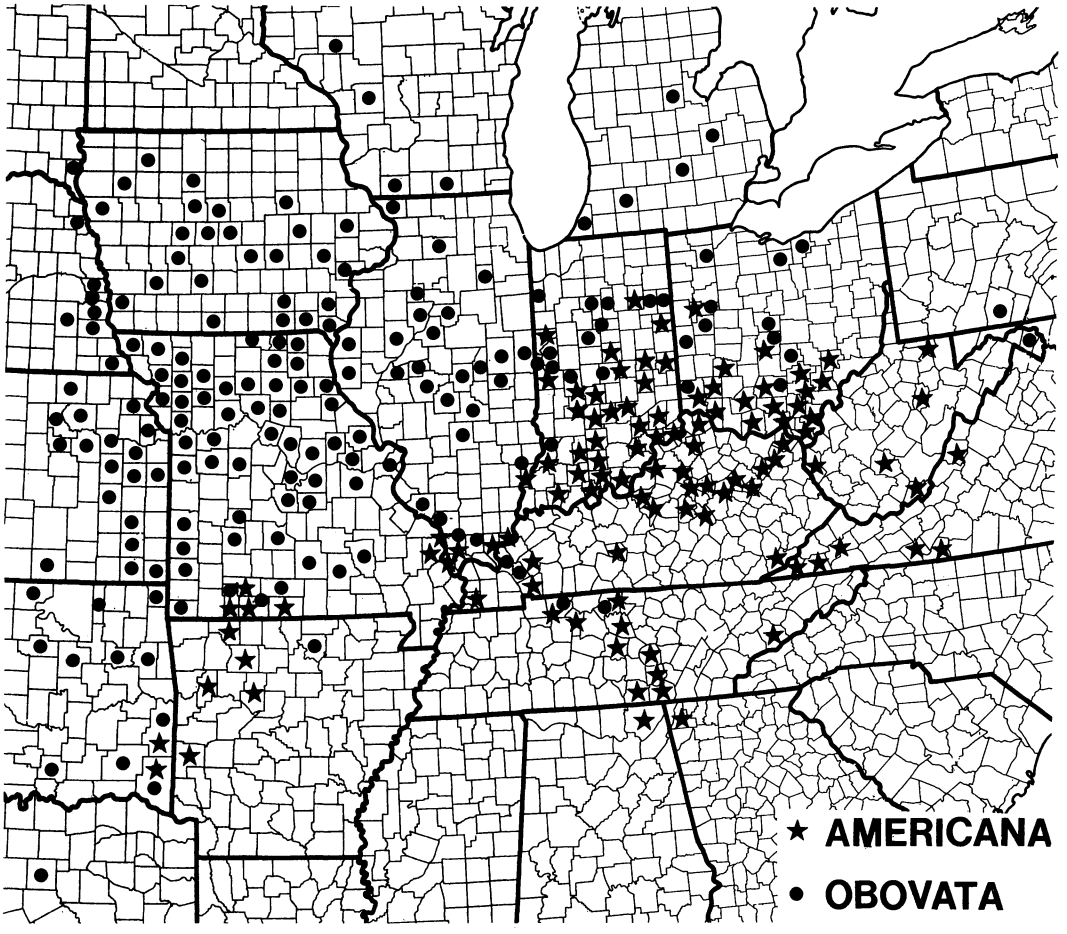

Fig. 3. Documented distribution of North American *Diarrhena*. See text for list of herbaria.

ing 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 ⅓ to ⅔ as long as second glume, less than ½ as long as first lemma, lanceolate, glabrous or scaberulous near apex of keel. *Lemmas* awnless, ± rounded on the back, chartaceous; nerves three, 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, ½ 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 base normally present; mature fruit swollen and spreading lemma and palea.

Summer and 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

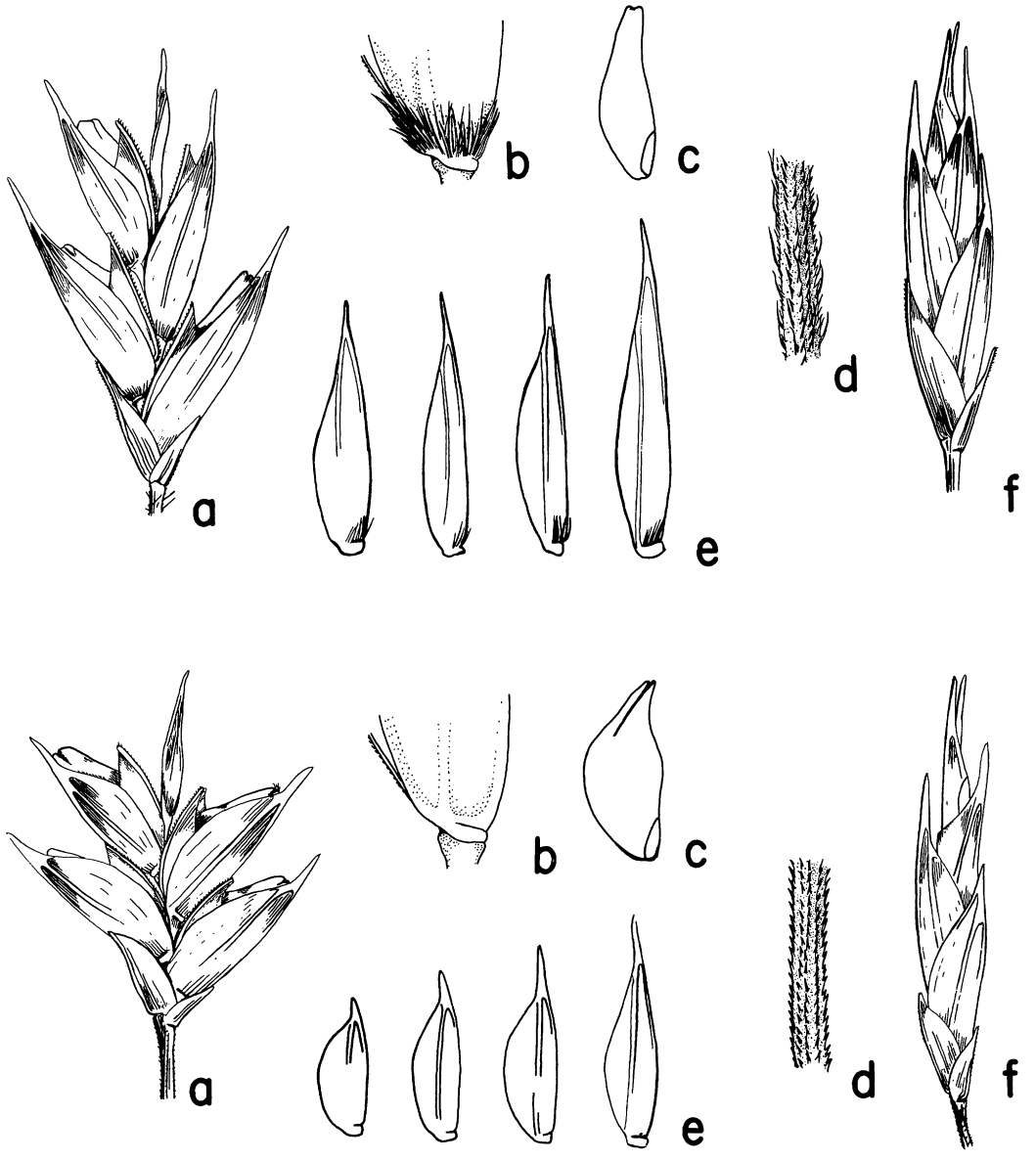

Fig. 4. Illustrations of North American *Diarrhena*. Top—*D. americana*. (a) mature spikelet (×5); (b) callus of lemma (×20); (c) caryopsis (×5); (d) inflorescence axis (×20); (e) lemmas (×5); (f) immature spikelet (×5). Bottom—*D. obovata*. (a) mature spikelet (×5); (b) callus of lemma (×20); (c) caryopsis (×5); (d) inflorescence axis (×20); (e) lemmas (×5); (f) immature spikelet (×5).

gradually tapering into a cusp at apex, those of first floret 7.1–10.8 mm long; mature fruit 1.3–1.8 mm broad, gradually tapering into a broad, blunt beak (Fig. 4, top) . *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 bottlenose-shaped beak (Fig. 4, bottom). ..... *D. obovata.*

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

Festuca diandra Michx., Fl. bor.-amer. 1: 67. 1803. (Type: P!). A later homonym of *Festuca diandra* Moench (1794), *fide* Anderson, 1958.

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

Festuca americana Michx. ex Beauv., Ess. Agrostogr. 162. 1812. Name only.
Korycarpus arundinaceus Zea ex Lag., Gen. sp. pl. Nov. 4. 1816.
Roemeria zeae Roem. & Schult., Syst. veg. 1: 61, 287. 1817.
Diarina sylvatica Raf. J. Phys. Chim. 89: 104. 1819. Based on *Festuca diandra* Michx.
Diarrhena diandra Wood, Class-book bot. Ed. 2. 612. 1847. Based on *Festuca diandra* Michx.
Corycarpus diandrus Kuntze, Rev. gen. pl. 2: 772. 1891. Based on *Festuca diandra* Michx.
Diarrhena festucoides Fernald, Rhodora. 34: 204. 1932. Based on *Diarina festucoides* Raf.
Diarrhena arundinacea Rydb., Fl. Plains 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 sometimes 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; (3.8–)5.3–10.8 mm long, first lemma (6.0–)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, very rarely some florets glabrous. *Paleas* glabrous or scaberulous, scabrous along upper ⅔ 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).

2. ***Diarrhena obovata*** (Gleason) Brandenburg in Brandenburg *et al., 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 surface 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 ovate, 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 ½ of keel; apex shallowly notched to bifid with notch 0.05–0.3(–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.

AXELROD, D. I. 1985. Rise of the grassland biome, central North America. Bot. Rev. 51: 163–201.

BRANDENBURG, D. M. 1985. Systematic studies in the Poaceae and Cyperaceae. Doctoral dissertation, University of Oklahoma, Norman.

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

CLAYTON, W. D. AND S. A. RENVOIZE. 1986. Genera graminum. Kew Bulletin additional series XIII. Her Majesty's Stationery Office, London.

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.

———. 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.

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

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*. Bot. 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.

TSVELEV, N. N. 1983. Grasses of the Soviet Union, Part II [translated from Russian by B. R. Sharma]. Oxonian Press Pvt. Ltd., New Delhi.

———. 1989. The system of grasses (Poaceae) and their evolution. Bot. Rev. 55(3): 141–204.

Appendix A. OTU's used in numerical analyses of North American *Diarrhena*. OTU designation, county, state abbreviation; *collector, collection number* [herbarium abbreviation].

AMERICANA: A1—Vinton, OH; *O'Dell, 1368* [BHO]. **A2**—Hamilton, IN; *Potzger, 9317* [ILL]. **A3**—Cheatham, TN; *Svenson, 10376* [US]. **A4**—Jefferson, IN; *Young, s.n.* [PH]. **A5**—Knox, IN; *Deam, 41741* [PH]. **A6**—Johnson, IL; *Ahles, 6955* [ILL]. **A7**—Johnson, IL; *White, 1407* [SIU]. **A8**—Pope, IL; *Hopkins, 613* [SIU]. **A9**—Gallia, OH; *Herrick, s.n.* [OS]. **A10**—Butler, OH; *Werth, OX26b49* [MU]. **A11**—Highland, OH; *Cusick, 21075* [MU]. **A12**—LeFlore, OK; *Means, 3974* [OKLA]. **A13**—Parke, IN; *Buser, 3125* [IND]. **A14**—Putnam, IN; *Deam, 7422* [IND]. **A15**—Warren, IN; *Deam, 11882* [IND]. **A16**—Ripley, IN; *Friesner, 21116* [MO]. **A17**—Vermillion, IN; *Hermann, 8446* [GH]. **A18**—Orange, IN; *Deam, 17322* [IND]. **A19**—Alexander, IL; *Ahles, 6753* [ILL]. **A20**—Stone, MO; *Steyermark, 81971* [UMO]. **A21**—Lawrence, OH; *Silberhorn, 2267* [KE]. **A22**—McCurtain, OK; *Taylor, 24665* [KANU]. **A23**—Marion, TN; *Clark & Ramseur, 1120* [NCU]. **A24**—Jackson, AL; *Kral, 47574* [NCU]. **A25**—Menifee, KY; *Conrad, 501* [NCU]. **A26**—Polk, AR; *MacRoberts, 1891* [TAES]. **A27**—Mercer, KY; *Wharton, 9205* [MEM]. **A28**—Trigg, KY; *Athey, 3159* [MEM]. **A29**—Orange, IN; *Tryon, 2022* [MIN]. **A30**—Fayette, WV; *Grafton & McGraw, s.n.* [WVA]. **A31**—Upshur, WV; *Grose, s.n.* [WVA]. **A32**—Carrol, VA; *Benedict, 3533* [VPI]. **A33**—Crawford, IN; *Potzger, 7739* [ND]. **A34**—Scott, IN; *Deam, 18892* [IND]. **A35**—Hamilton, IN; *Friesner, 17354* [GH]. **A36**—Crawford, IN; *Siegler, Smith & Spencer, 11859a* [ILL]. **A37**—Athens, OH; *Cusick & Ortt, 17996* [KE]. **A38**—Greene, OH; *Anliot, s.n.* [OS]. **A39**—Scioto, OH; *Jones, s.n.* [OS].

OBOVATA: O01—Shelby, OH; *Cusick, 15500* [OS]. **O02**—Miami, IN; *Deam, 46183* [IND]. **O03**—Henry, IA; *LeLong, 2239* [ISC]. **O04**—Livingston, KY; *Athey, 2636* [SIU]. **O05**—Franklin, OH; *Werner, s.n.* [OS]. **O06**—Johnson, IL; *White, 1898* [SIU]. **O07**—Auglaize, OH; *Wetzstein, s.n.* [MU]. **O08**—Darke, OH; *Cusick, 15575* [MU]. **O09**—Huron, OH; *Jones 67-9-25-1163* [MU]. **O10**—McCurtain, OK; *Tyrl, Lofgren, Brunken & Perino, 53* [OKL]. **O11**—Washington, OK; *McDonald, 974* [OKLA]. **O12**—Cherokee, OK; *Wallis, 5364* [OKLA]. **O13**—Ross, OH; *Bartley & Pontius, 621* [NY]. **O14**—Greene, IA; *Monson, 588* [ISC]. **O15**—Knox, IN; *Deam, 24165,* [IND]. **O16**—Clinton, IN; *Deam, 50656* [IND]. **O17**—Vermilion, IL; *Jones, 13245* [ILL]. **O18**—Putnam, IN; *Grimes, 769* [ILL]. **O19**—Tazewell, IL; *McDonald, s.n.* [ILL]. **O20**—Shelby, IL; *Shildneck, C-12232* [ILL]. **O21**—Randolph, MO; *Conrad, Dimit & Walker, 8558* [UMO]. **O22**—Jackson, MO; *Bush, s.n.* [UMO]. **O23**—Linn, MO; *Crookshanks, 265* [UMO]. **O24**—Peoria, IL; *Chase, 8386* [MICH]. **O25**—Berrien, MI; *Billington, s.n.* [MICH]. **O26**—Cass, IA; *Fay, 5148* [KANU]. **O27**—Cherokee, KS; *McGregor, 33425* [KANU]. **O28**—Jefferson, WV; *Core, s.n.* [WVA]. **O29**—Sumner, TN; *Rogers & Rogers, 40828* [TENN]. **O30**—Wilson, TN; *Rogers & Rogers, 40882* [FLAS]. **O31**—Shawnee, KS; *Volle, 824* [KANU]. **O32**—Otoe, NE; *Stephens, 17588* [KANU]. **O33**—Cherokee, OK; *Waterfall, 9633* [TEX]. **O34**—Howard, MO; *Steyermark, 26295* [MO]. **O35**—Bedford, PA; *Berkheimer, 20673* [PH]. **O36**—Vermillion, IN; *Deam, 37923* [PH]. **O37**—Riley, KS; *Norton, 936* [GH]. **O38**—Leavenworth, KS; *Wagenknecht, 3369* [GH]. **O39**—Cass, IL; *Geyer, s.n.* [MO].