

A Taxonomic Revision of the Eastern North American and Eastern Asian Disjunct Genus *Brachyelytrum* (Poaceae): Evidence from Morphology, Phylogeography and AFLPs

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ABSTRACT. Morphological and phylogeographical data support the recognition of three distinct species in the genus *Brachyelytrum*: *B. japonicum*, *B. erectum*, and *B. aristosum*. *Brachyelytrum japonicum* is confined to eastern Asia and is characterized by narrow leaf blades (0.5–0.8 cm wide), long lower glumes (0.2–2.0 mm long), and long rachillas (6.8–8.8 mm long). *Brachyelytrum erectum* is distributed throughout much of the eastern United States, from northwestern Minnesota south to central Louisiana, east to northern Florida and north to northeastern New York. *Brachyelytrum erectum* is characterized by long hispid hairs (0.2–0.9 mm long) on the veins of the lemma, wide lemmas (0.8–1.8 mm wide), and a conspicuous lemma mid-vein. *Brachyelytrum aristosum* has a more northern distribution, occurring in southern Canada from southern Ontario to Newfoundland, the northern adjacent United States and through the Appalachian mountains to northwestern North Carolina. *Brachyelytrum aristosum* is characterized by short scaberulous hairs (0.06–0.2 mm long) on the lemma and narrow lemmas (0.7–1.4 mm wide) that are weakly veined. The distinctiveness of *B. erectum* and *B. aristosum* is further supported by amplified fragment length polymorphism (AFLP) data. We include a key to the taxa, synonymies, descriptions, and representative specimens. This study represents a recent monographic study of an eastern North American and eastern Asian disjunct genus.

Brachyelytrum P. Beauv. (Poaceae: Pooideae: Brachyelytreae) is a small genus of grasses that grows in mesic to dry upland forests in eastern North America and eastern Asia. It is one of several grass genera that exhibits this classic intercontinental disjunction pattern (Koyama and Kawano 1964). *Brachyelytrum* can be distinguished from other grass genera by a combination of several characters including leaf blades that are constricted at the base, one-flowered spikelets with a bristle-like rachilla extension, reduced glumes, and a linear caryopsis with a beak with two terminal styles (Clayton and Renvoize 1986).

Brachyelytrum is a rather enigmatic genus and has a complex classification history. Early authors recognized various morphological similarities between *Brachyelytrum* and other pooid/festucoid genera, such as the absence of microhairs, parallel-sided subsidiary cells, and the presence of an epiblast, which resulted in the genus being placed in various pooid/festucoid tribes including Agrostideae (Bentham 1881; Hitchcock 1951), Poeae (Pilger 1954), Bromaeae (Ohwi 1942), and Brachyelytreae (Ohwi 1941; Tateoka 1957a; Stebins and Crampton 1961; Booth 1964; Gould and Shaw 1983). Tateoka (1957b), however, placed it in subfamily Arundinoideae. Further studies of morphology revealed that *Brachyelytrum* was quite distinct from other pooids and exhibited several characters typical of bambusoid genera, including the presence of a scutellar cleft in the embryo, thick walled parenchyma cells and dumbbell shaped silica bodies, seedlings with a short

first internode and no adventitious roots, uniformly sized root epidermal cells, and leaves with inconspicuous osmophilic layers in the mesostome sheath cell walls (Reeder 1957, 1962; Tateoka 1957a, 1960; Brown 1958; Macfarlane and Watson 1980; Campbell et al. 1986). Cytological studies revealed a base chromosome number of $x = 11$ (Brown 1950; Bowden 1960), similar to that found in some of the herbaceous bamboos (Calderon and Soderstrom 1980; Hunziker et al. 1982). With knowledge of these apparent bambusoid affinities, subsequent authors left *Brachyelytrum* unplaced (Macfarlane and Watson 1980; Campbell 1985) or treated it as a member of subfamily Bambusoideae (Clayton and Renvoize 1986; Tucker 1988; Watson and Dallwitz 1992). This bambusoid placement was later weakly supported by chloroplast DNA restriction-site variation (Davis and Soreng 1993). However, subsequent results from a combined phylogenetic analysis of chloroplast DNA restriction site data and morphological characters rejected *Brachyelytrum* as a member of subfamily Bambusoideae and suggested that it should be included in a more broadly defined Pooideae or recognized as the sole genus in its own subfamily sister to the Pooideae (Soreng and Davis 1998). Other cladistic analyses of morphological data (Kellogg and Campbell 1987; Kellogg and Watson 1993), chloroplast DNA restriction site variation with morphology (Soreng and Davis 2000), and DNA sequence data from *ndhF* (Clark et al. 1995; Catalan et al. 1997), ITS (Hsiao et al. 1999), *matK* (Hilu et al. 1999), and the *rpl16* intron (Zhang

2000) have confirmed that *Brachyelytrum* belongs in subfamily Pooideae. This phylogenetic placement is maintained in the most recent classifications of the grass family (Tsvelev 1989; Soreng et al. 2000; Grass Phylogeny Working Group 2001). *Brachyelytrum* represents the deepest split in the Pooideae (Grass Phylogeny Working Group 2001), and the bambusoid-like characters that caused earlier confusion in the classification of the genus have been explained as retained plesiomorphies (Catalan et al. 1997).

Despite a well-resolved phylogenetic position, the taxonomy of the genus remains controversial, and like many other eastern Asian and eastern North American disjunct genera has not been studied in detail (Wen 1999). Past treatments of the genus have varied widely because of a high degree of similarity among taxa. Much confusion has arisen regarding both the number and rank of taxa as well as the criteria used to define them. In North America, *Brachyelytrum* has been variously treated as one species (e.g. Jones and Fuller 1955; Massey 1961; Braun 1967; Radford et al. 1968; Rousseau 1974; Catling et al. 1985; Harvill et al. 1986; Jones and Coile 1988; Smith 1988; Ownbey and Morley 1991; Thomas and Allen 1993; Swink and Wilhelm 1994; Wunderlin 1998), as a single species with two varieties (Babel 1943; Fassett 1951; Lakela 1965; Pohl 1966; Stephenson 1971; Wherry et al. 1979; Dore and McNeill 1980; Gleason and Cronquist 1991; Rouleau and Lamoureux 1992), as one subspecies with two varieties (Koyama and Kawano 1964), and as two distinct species (Tucker 1988; Yatskievych 1999; Magee and Ahles 1999). Asian plants have been variously treated as a variety (Hong 1993) or a subspecies of the North American species (Koyama and Kawano 1964; Koyama 1987; Shouliang and Philips in prep.), and as a distinct species (Steward 1958; Ohwi 1965; Tucker 1988). Among North American taxa, Babel (1943) emphasized differences in the length of hairs on the lemma, while Koyama and Kawano (1964) discounted this character and emphasized differences in lemma size, leaf width, and the degree of ramification of panicle branches. Stephenson (1971) cited differences in anther length, length of lemma pubescence, and density of leaf cilia as well as ecological differentiation, whereas Tucker (1988) emphasized differences in density of leaf cilia, lemma hair length, palea length, upper glume length, and anther length. The Asian taxon has been separated from the North American taxa in having narrower leaves and longer glumes (Koyama and Kowano 1964).

While preparing a treatment of North American *Brachyelytrum* for 'The Catalogue of New World Grasses' (Soreng et al. 2000), the third author was unable to consistently separate the taxa using characters cited in previous treatments. A reevaluation of the characters used in past taxonomic treatments of the genus there-

fore seemed necessary. Here we present the results of a macromorphological and phytogeographical study of *Brachyelytrum* from throughout its geographic range, and provide molecular amplified fragment length polymorphism (AFLP) data for North American taxa. We then present a taxonomic revision of the genus including a key to the taxa, synonymies, descriptions, and representative specimens. We recognize three distinct species in *Brachyelytrum*: one from Asia [*B. japonicum* (Hack.) Matsum. ex Honda] and two [*B. erectum* (Schreb.) P. Beauv. and *B. aristosum* (Michx.) Trel.] from eastern North America. This study represents one of few detailed morphological comparisons of a genus that displays the classic eastern North American—eastern Asian disjunct pattern.

MATERIALS AND METHODS

Morphological observations and lists of representative specimens were based on herbarium specimens from ALTA, GH, HAST, ISC, MO, and US (herbarium abbreviations follow Index Herbariorum <http://www.nybg.org/bsci/ih/search>) and field collections made in the summers of 2001 and 2002 in Maryland, Ohio, Pennsylvania, Virginia, West Virginia, and Wisconsin. Approximately 1000 specimens were observed in this study. These specimens were used to plot geographic distributions and were all carefully examined to ensure consistency in our taxonomic treatment. A sample of these specimens is cited in the representative specimens examined (see Taxonomic Treatment).

Multivariate Analyses. A subset of 110 mature and complete specimens representing a wide range of morphological and geographical variation in the genus was chosen for detailed morphometric study. Specimens were initially placed into groups according to previous taxonomic treatments based on the size and distribution of lemma hairs and geography. This resulted in four morphological groups: three from North America (*B. erectum* [specimens with long hairs on the lemma veins], *B. aristosum* [specimens with short hairs on the lemma veins], and plants that were initially considered to be intermediate specimens [specimens with long hairs between the lemma veins]) and one from Asia (*B. japonicum* [specimens with narrow leaves]). After initial scoring, the lemma hair density character used to delineate supposed North American intermediates proved too variable to be taxonomically useful, and these plants were subsequently treated as belonging to *B. erectum*, based on their lemma hair length. Nineteen morphological characters (Table 1) were measured on a total of 110 specimens (12 *B. japonicum*; 39 *B. aristosum*; 59 *B. erectum*). Specimens used in the analyses are denoted by an asterisk (*) in the representative specimens examined (see Taxonomic Treatment). The small sample size for *B. japonicum* reflects the paucity of specimens available in North American herbaria. Morphological characters were scored and included in the analyses for the type specimens for each of the three species in order to apply the correct names to the appropriate morphological entities. Summary statistics including means, standard deviation, and ranges were calculated for all characters. Raw data from the actual measurements is available from the corresponding author. In the discussion of morphological characters, the taxonomic key, and the species descriptions, measurements for characters are reported as the mean \pm one standard deviation, with observed outliers included in parentheses.

For each specimen, measurements for reproductive characters were taken from one representative mature spikelet from the center of the largest inflorescence on each herbarium sheet. Panicle length was measured from the base of the lowermost spikelet to the apex of the panicle. Spikelet length was measured from the base of the callus to the tip of the awn. Lemma width was mea-

TABLE 1. Morphological characters measured on *B. japonicum*, *B. aristosum* and *B. erectum* and their means \pm standard deviations and ranges (in parentheses). *N* = sample size.

Character	<i>B. japonicum</i> (<i>N</i> = 12)	<i>B. aristosum</i> (<i>N</i> = 39)	<i>B. erectum</i> (<i>N</i> = 59)
Spikelet length (mm)	24.4 \pm 3.6 (20.0–30.0)	29.3 \pm 3.3 (23.0–36.0)	32.6 \pm 3.5 (25.0–42.0)
Lemma width (mm)	0.9 \pm 0.1 (0.7–1.2)	1.0 \pm 0.2 (0.7–1.4)	1.3 \pm 0.2 (0.8–1.8)
Awn length (mm)	14.4 \pm 3.0 (9.5–19.4)	19.8 \pm 2.8 (14.0–26.0)	23.0 \pm 4.0 (14.3–32.4)
Rachilla length (mm)	7.8 \pm 0.6 (6.8–8.8)	5.6 \pm 0.7 (4.0–6.9)	6.3 \pm 0.9 (3.9–8.1)
Palea length (mm)	9.6 \pm 1.0 (7.6–11.4)	9.4 \pm 1.0 (7.7–11.5)	9.3 \pm 1.1 (7.1–11.9)
Panicle length (cm)	12.4 \pm 2.8 (8.3–18.0)	12.5 \pm 3.0 (6.6–17.5)	11.7 \pm 2.6 (5.5–18.5)
Branches/panicle (no.)	2.8 \pm 1.1 (1.0–5.0)	3.3 \pm 1.4 (0.0–7.0)	2.8 \pm 1.2 (0.0–6.0)
Spikelets/panicle (no.)	14.6 \pm 3.9 (9.0–19.0)	23.7 \pm 10.7 (8.0–55.0)	17.7 \pm 6.8 (4.0–35.0)
Lower glume length (mm)	1.0 \pm 0.6 (0.2–2.0)	0.3 \pm 0.1 (0.1–0.9)	0.5 \pm 0.2 (0.1–1.1)
Upper glume length (mm)	2.6 \pm 1.0 (0.8–4.8)	1.2 \pm 0.5 (0.6–3.0)	2.2 \pm 1.3 (0.2–7.0)
Lemma hair length (mm)	0.1 \pm 0.0 (0.1–0.2)	0.11 \pm 0.03 (0.1–0.2)	0.6 \pm 0.2 (0.2–0.9)
Lemma hair density (no. per 2 mm)	14.6 \pm 4.0 (9.0–23.0)	16.1 \pm 5.2 (7.0–31.0)	9.9 \pm 2.7 (5.0–17.0)
Leaf blade length (cm)	10.7 \pm 2.3 (8.1–14.5)	10.8 \pm 2.2 (6.9–16.1)	12.9 \pm 1.9 (9.5–17.5)
Leaf blade width (cm)	0.6 \pm 0.1 (0.5–0.8)	1.2 \pm 0.2 (0.8–1.6)	1.4 \pm 0.3 (0.9–2.0)
Sheath length (cm)	4.4 \pm 0.6 (3.7–5.4)	6.1 \pm 1.6 (3.2–10.4)	5.1 \pm 1.0 (3.1–7.2)
Internode length (mm)	8.8 \pm 2.3 (4.2–11.7)	8.4 \pm 3.0 (3.9–15.5)	6.3 \pm 2.0 (3.5–12.3)
Macrohair density (no. per 2 mm)	5.9 \pm 4.5 (0–13.0)	7.1 \pm 4.4 (0.0–17.0)	1.7 \pm 2.6 (0.0–12.0)
Prickle hair density (no. per 2 mm)	10.9 \pm 8.2 (2–30.0)	13.2 \pm 5.6 (1.0–23.0)	16.2 \pm 5.8 (5.0–27.0)
Plant height (cm)	53.5 \pm 13.7 (37.5–76.0)	59.5 \pm 18.4 (28.5–96.0)	57.9 \pm 13.5 (34.5–102.0)

sured at the widest point of the lemma. Awn length was measured from the apex of the palea to the apex of the awn. Rachilla length and palea length were measured from the top of the callus to their apices. Lemma hair density was measured over a 2 mm distance along the keel vein at a point 4 mm from the base of the spikelet, and the longest lemma hair along this interval was measured to determine maximum lemma hair length. Leaf blade length was measured on the longest leaf blade; generally, this was the 4th leaf blade from the flag leaf (top), however in some cases the 3rd, 2nd, and 5th leaf blades were determined to be the longest. Leaf blade width was measured at the widest point of the longest leaf. Leaf sheath length and internode length were measured on the same longest leaf blade. Leaf macro hair (long hairs) and prickle hair (short teeth-like hairs usually described as scabrous) density were counted on the adaxial leaf margin over a 2 mm range at a point 4 cm from the base of the longest leaf blade. Plant height was measured from the base of the culm to the first branch of the inflorescence.

Multivariate statistical analyses were performed on the data set using SYSTAT[®] v.10 (Systat Software Inc., Richmond, CA). A discriminant analysis (DA) was performed using all three taxa to evaluate the taxonomic utility and importance of characters by determining which were most useful in maximally discriminating the three groups. All 19 morphological characters were used in

the DA since specimens could be placed into groups *a priori* using a qualitative character (prominence of the lemma mid-vein) and geography. Discriminant analyses have been used a lot in the taxonomic literature to evaluate the utility of potentially taxonomic informative characters and aid in the delimitation of species (e.g. Saarela and Ford 2001; Saez and Aldasoro 2003). Principal components analysis (PCA) was performed to assess morphological variation in the data and to assess phenetic similarities/dissimilarities among taxa. A second PCA was conducted using only the North American plants to look more closely at their morphological variation. The PCA used a correlation matrix of standardized variables from the data to give each character the same contribution to the overall variance in the analysis. Our morphological concepts of taxa were superimposed onto the resulting scatterplots to assess visually if our taxonomic concepts corresponded to morphologically distinct entities.

Micromorphology. Scanning electron microscopy (SEM) was employed to search for and illustrate taxonomically informative micromorphological characters on the lemma and the leaf surfaces. Mature spikelets from the center of the panicle were chosen from representatives of each taxon. Photographs were taken of the abaxial and adaxial sides of the lemma and the callus region. Leaf segments were obtained from the longest leaf on a plant, with photographs taken of both the abaxial and adaxial margins and

TABLE 2. *Brachyelytrum erectum* and *B. aristosum* populations used in AFLP analysis. Collections were made in the U.S.A. during 19–22 July 2001 by P.M. Peterson and J. M. Saarela. Voucher specimens are deposited at US.

<i>B. erectum</i> . 15790. Pennsylvania, Fayette Co.: ca. 2 miles E of Ohiopyle on Hwy. 381. 15774a,b. Virginia, Page Co.: 9 miles N of Hwy. 211 on Skyline Drive at entrance to Matthew's Arm Camp Ground, Shenandoah National Park. 15777. Virginia, Page Co.: ca. 10 ft. off path to Jeremy's Run, Elkwallow, Shenandoah National Park. 15779. West Virginia, Hardy Co.: 7 miles SW of Wardensville along road beside Lost River. 15786. West Virginia, Tucker Co.: 8 miles down road 13 from Canaan Heights along Red Run
<i>B. aristosum</i> . 15787. Maryland, Garrett Co.: Across street from 1815 Boiling Springs Road, near corner of Boiling Springs Road and Philsinger Road, ca. 2 mi. E of Deer Park. 15789. Pennsylvania, Fayette Co.: 1 mile NE of Farmington on Hwy. 281 towards Ohiopyle. 15791. Pennsylvania, Somerset Co.: along Ridge Trail ca. 6/10 mi. down Jones Run Road along Jones Run Creek, Laurel Hill State Park. 15792. Pennsylvania, Somerset Co.: ca. 3 miles W of Sipesville. 15793. Pennsylvania, Westmoreland Co.: ca. 0.5 miles W of Laughlinton on Hwy. 281. 15795. Pennsylvania, Cambria Co.: along Hwy. 160, 2.5 mi. N of Wilmore. 15796. Pennsylvania, Cambria Co.: ca. 4 miles from Portage on Hwy. 164. 15797. Pennsylvania, Bedford Co.: ca. 3 miles S of Rainsburg on Hwy. 326. 15783. West Virginia, Grant Co.: 7 miles leaving Hwy. 28. 15785. West Virginia, Grant Co.: 8 miles from Hwy. 28

surfaces. Samples were mounted onto aluminum stubs with conductive carbon adhesive discs, coated with 20–25nm gold/palladium in a Cressington Scientific 108a-SE sputter coater, and photographed in high vacuum mode on a Philips XL-30 ESEM with LaB6 (10 kV accelerating voltage).

Phytogeography. Specimen label data and distribution records from the literature (Mohr 1901; Deam 1940; Gates 1940; Fassett 1951; Jones and Fuller 1955; Massey 1961; Lakela 1965; Pohl 1966; Braun 1967; Radford et al. 1968; Rousseau 1974; Wherry et al. 1979; Catling et al. 1985; Harville et al. 1986; Jones and Coile 1988; Smith 1988; Chester et al. 1993; Dore and McNeill 1980; Ownbey and Morley 1991; Rouleau and Lamoureux 1992; Thomas and Allen 1993; Swink and Wilhem 1994; Wunderlin 1998; Yatskievych 1999; Shouliang and Philips, in prep.) were used to determine the geographical distribution of characters and taxa. Additional locality data from specimens of *B. japonicum* were obtained from the Tokushima Prefectural Museum, Japan (TKPM) (<http://www.museum.comet.go.jp/e.museum.htm>). Latitude and longitude coordinates for exact locations and counties in North America were obtained from label information or from the Geographical Names of Canada (<http://geonames.nrcan.gc.ca/english/cgndb.html>) and the United States Geographical Survey Geographic Names Information System (GNIS) (<http://geonames.usgs.gov/gnishome.html>). Distribution maps were created in ArcView 3.0.

Amplified Fragment Length Polymorphisms (AFLPs). AFLP analysis was conducted to determine if North American taxa could be differentiated genetically. The AFLP method provides markers that are more variable than some other methods (e.g. restriction site studies; allozyme studies) and is more robust and consistent than other PCR based methods (e.g. RAPDs), and it has been used previously to genetically assess species boundaries (e.g. Peterson et al. 2002; Coart et al. 2002; van den Berg et al. 2002).

Leaf tissue was collected in the field from six individuals of *B. erectum* and 10 individuals of *B. aristosum* from 15 geographically distinct populations (Table 2) and dried using silica gel. Species were identified using the morphological criteria obtained from this study. Voucher specimens from each population sampled are deposited at US. Total genomic DNA was extracted using a modified

version of the CTAB protocol described by Doyle and Doyle (1987). Various attempts to extract DNA from specimens of *B. japonicum* were unsuccessful. Individuals used in the AFLP analysis were not included in the multivariate analysis because they were collected after the multivariate component of the study was complete.

AFLP analysis was performed according to Vos et al. (1995) using fluorescently labeled markers (Applied Biosystems, Foster City, CA). Initially, 500 ng of genomic DNA was digested with *EcoRI* and *MseI* restriction enzymes and double-stranded adaptors were ligated to the restriction fragments to create primary templates for subsequent amplification. Primary templates were pre-amplified with AFLP primers with an additional single nucleotide at the 3' end. Pre-amplified fragments were selectively amplified with fluorescently labeled *EcoRI* primers having three selective nucleotides at the 3' end and *MseI* primers having three selective nucleotides at the 3' end. Initially, 30 *EcoRI*: *MseI* primer combinations were tested on one individual each of *B. erectum* and *B. aristosum* to identify primer pairs that could be used to distinguish the two species genetically. Selective PCR amplification of all 16 individuals of *Brachyelytrum* was performed using the following six M+3 / E+3 primer combinations, where M = 5' GATGAGTCTGAGTAA and E = 5' GACTGCGTACCAATTC: (i) M-CAA/E-ACT; (ii) M-CAA/E-CTA; (iii) M-CAA/E-CTG; (iv) M-CTA/E-AAC; (v) M-CTG/E-ACC; (vi) M-CAA/E-ACA. AFLP products were run on an ABI 377 Prism Automatic sequencer (PE Applied Biosystems, Inc.) and viewed using GeneScan® software.

Robust AFLP bands that were determinable with minimum ambiguity were scored for presence (0) and absence (1). From this data matrix, genetic relationships among the 16 individuals were reconstructed from a Nei-Li association matrix with the Minimum Evolution optimality criterion in PAUP*v4.0b (Swofford 1999). The tree was not rooted and bootstrap support for the tree was estimated based on 100 replicates.

Ecology. For each population studied in the field, we noted vascular plant associates and local site conditions. Most of our field observations were conducted where the ranges of *B. erectum* and *B. aristosum* are sympatric (Table 2). We searched all populations for the presence of more than one species of *Brachyelytrum* and for the occurrence of possible intermediates.

RESULTS

Multivariate Analyses. A scatterplot of the scores on canonical factors I and II from discriminant analysis of 19 morphological characters for members of *Brachyelytrum* depicts three clearly distinct groupings of individuals (Figure 1). Each of the groups have significantly different morphological characteristics (Wilks' lambda = 0.0176; F = 30.64; df = 38, 178; p < 0.0001). Ninety-nine percent of all individuals were properly classified in the DA, with only one specimen of *B. erectum* being misclassified. The type specimen of *B. japonicum* was referable to the cluster positioned low on factor I and high on factor II, while the type of *B. aristosum* was referable to the cluster of specimens positioned low on factors I and II. The type specimen of *B. erectum* assumed a somewhat intermediate position between two major specimen clusters, though it was classified by the DA to belong in the group of individuals that are positioned high on factor I and low on factor II. Variables with the highest loadings on factor I were lemma hair length (6.072), lemma width (1.730), and leaf blade width (1.262), and on factor II were leaf blade width (-2.560), lower glume length (2.020), rachilla length (1.198) and lemma width (-1.987). These

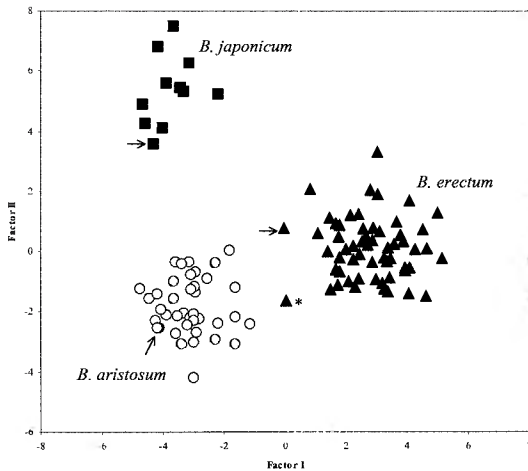


FIG. 1. Scatterplot of scores on canonical factors 1 vs. canonical factor II from discriminant analysis of 110 specimens of *Brachyelytrum*. Squares represent individuals of *B. japonicum* (N = 12), circles represent *B. aristosum* (N = 39), and triangles represent *B. erectum* (N = 59). Type specimens are indicated with an arrow (→). The individual denoted by an asterisk (*) was misclassified in the analysis.

characters are considered diagnostic and are most useful for delineating and circumscribing taxa. Based on the positions of the type specimens in the analysis, the name *B. japonicum* is referable to plants with narrow leaf blades, long lower glumes, long rachillas; the name *B. aristosum* is referable to plants with short lemma hairs, narrow lemmas, and narrower leaf blades; and the name *B. erectum* is referable to plants with long lemma hairs, wide lemmas and wide leaf blades.

Principal components analysis of the three taxa graphically summarizes the phenetic similarities and differences among individuals of *Brachyelytrum* (Fig. 2a). Though there is slight overlap between groups there are three clusters evident in a scatterplot of the scores on principal components I and II. This suggests the existence of three different morphological entities present in the data set. Type specimens of *B. japonicum* and *B. aristosum* fell within their respective clusters, while the type specimen of *B. erectum* appeared more closely allied with specimens of *B. aristosum*. The first two principal component axes accounted for 41.9% of the variation, with component I accounting for 21.5% and component II accounting for 20.4%. The third principal component accounted for 15.5% of the variation in the data set, and offers no further separation of groups. Principal component axis II is a size axis, with small plants grouping low on the axis and larger plants grouping higher on the axis. The PCA indicates that plants of *Brachyelytrum japonicum* are smallest in size, individuals of *B. aristosum* are intermediate in size, and individuals of *B. erectum* tend to be the largest. As axis II increases leaf blade length and width,

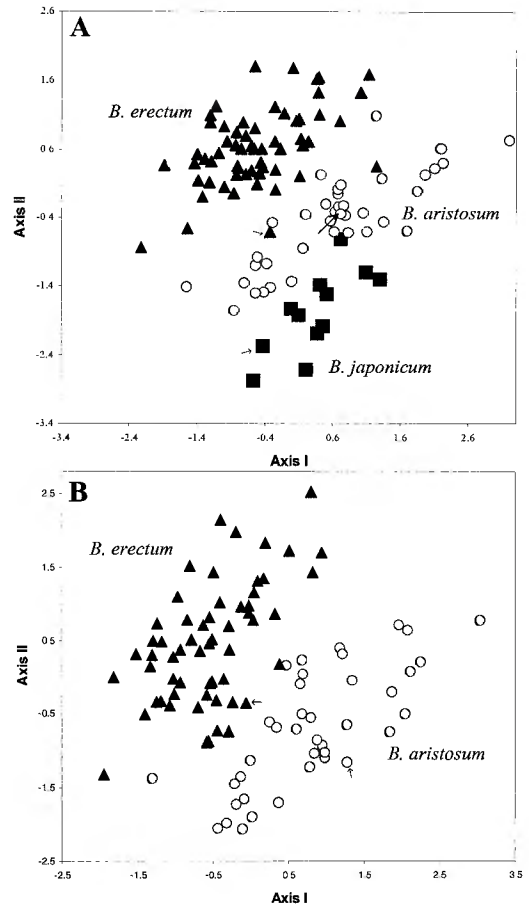


FIG. 2. Scatterplot of scores on principal component 1 vs. principal component 2 from PCA of specimens of *Brachyelytrum*: A. *B. japonicum* (squares; N = 12), *B. aristosum* (circles; N = 39) and *B. erectum* (triangles; N = 59); and B. *B. aristosum* (circles; N = 39) and *B. erectum* (triangles; N = 59). Type specimens are indicated with an arrow (→).

spikelet length, lemma width, awn length, lemma hair length, and lemma hair density increase (eigenvalues not shown). These trends are reflected in the measurements of morphological characters (Table 1). For example, spikelet length ranges from 24.4 ± 3.6 mm in *B. japonicum*, 29.3 ± 3.3 mm in *B. aristosum*, and 32.6 ± 3.5 mm in *B. erectum* (Table 1). The large degree of spread in the scatterplot suggests that each species contains considerable morphological variability.

Principal components analysis of only the North American taxa provided a clearer separation of these two entities (Fig. 2b). A total of 44.1% of the variation in the data set was accounted for by the first two principal component axes, with component I accounting for 23.4% and component II accounting for 20.7%. Component III accounted for only 12.8% of the variation and offered no further separation of groups. Trends in the data are similar to those observed when

all three taxa were included. The type of *B. aristosum* was nested in the center of its respective cluster, while the type of *B. erectum* was positioned on the periphery of its group, just outside the range of variation observed in *B. aristosum* (Fig. 2b).

Morphological Characters. According to the discriminant analysis, five of the 19 morphological characters measured on *Brachyelytrum* are useful for delimiting species. Means, standard deviations, and ranges for each quantitative character measured are given in Table 1. In North America, *B. aristosum* and *B. erectum* are easily and consistently distinguished by the morphology and distribution of the longest hairs on the surface of the lemma. This character is consistent across the entire surface of the lemma except for the basal portion directly above the callus region. *Brachyelytrum erectum* is characterized by hispid hairs distributed on the surface of the lemma veins whose maximum length ranges from (0.2–) 0.4–0.8 (–0.9) mm long (Table 1, Fig. 3). The morphology of the surface of the lemma between the veins in *B. erectum* is variable, with some specimens being glabrous, some with scabrous hairs similar to those found in *B. aristosum*, and others with longer hairs similar to those found on the veins. The mid-vein of the lemma in *B. erectum* is conspicuous and is generally much more prominent than the other veins on the surface of the lemma. *Brachyelytrum aristosum* is characterized by scaberulous hairs distributed on the surface and veins of the lemma whose maximum length ranges from (0.06–) 0.08–0.14 (–0.2) mm long (Table 1, Fig. 3). The lemma veins in *B. aristosum* are inconspicuous and the mid-vein is generally similar in morphology to the other veins. North American species are further distinguished by the width of lemma. The lemma in *B. erectum* is wider, ranging from (0.8–)1.1–1.5(–1.8) mm wide, while the lemma in *B. aristosum* is narrower ranging from (0.7–) 0.8–1.2 (–1.4) mm wide (Table 1). Overall, individuals of *B. erectum* tend to be larger plants on average than those of *B. aristosum* with longer spikelets, longer awns, longer upper glumes, and longer and wider leaf blades (Table 1).

Stephenson (1971) and Tucker (1988) reported that anther length could be used to discriminate North American taxa, with anthers 5–6 mm for *B. erectum* and 2.5–4 (–5) mm for *B. aristosum*. Based on a limited sample mostly from our field-collected material (anthers were not consistently present in our specimens and so were excluded from the multivariate analysis), this seems to hold. We observed that anthers are larger in *B. erectum* [4.37 ± 1.1 (n = 5)] and smaller in *B. aristosum* [2.73 ± 0.73 (n=19)]. This character has some taxonomic utility, but it is of limited practical use since anthers are rarely preserved on herbarium specimens and are only available for a relatively short period of time in the field. Stephenson (1971) and Tucker (1988)

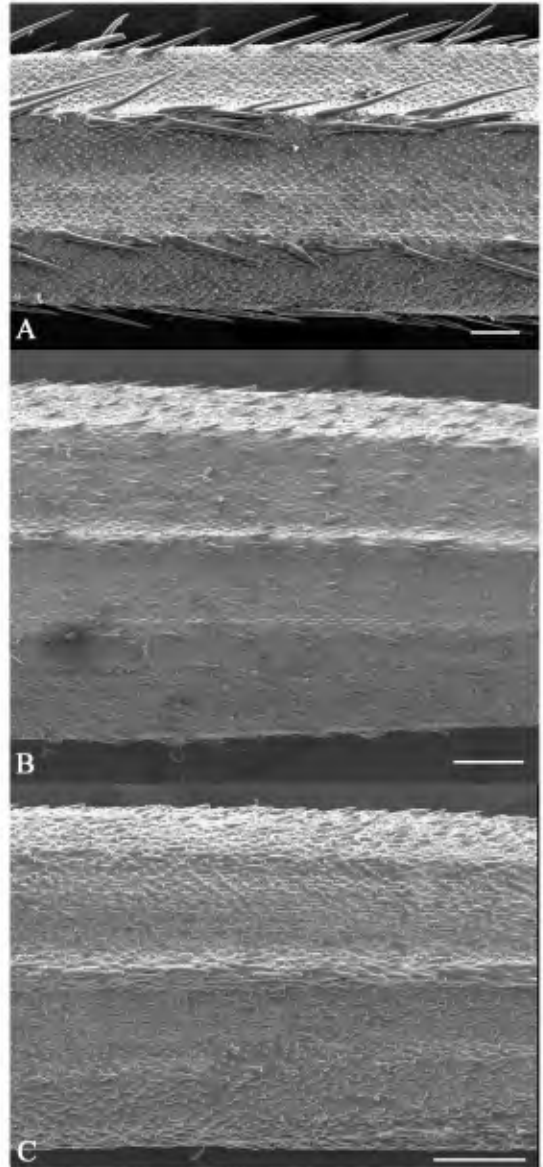


FIG. 3. Dorsal surface of the lemma. A. *Brachyelytrum erectum* (Wadmond, Slinners & Stearns s.n. US). B. *B. aristosum* (Peterson 15797 & Saarela US). C. *B. japonicum* (Togasi 1196 US). Scale bar = 200 μ m.

also reported taxonomically useful differences in the length of the palea and in the density of hairs on the leaf margin. We found no difference in palea length among all three taxa (Table 1). We did observe a difference in density of hairs on the margins of the leaf, although there was considerable overlap in this character, making it taxonomically unreliable (Table 1).

Brachyelytrum japonicum is easily distinguished from North American plants by its narrow leaf blades [0.5–0.7 (–0.8) mm wide], long lower glumes [(0.2–) 0.4–1.6 (–2.0) mm long], and long rachillas [(6.8–) 7.2–8.4

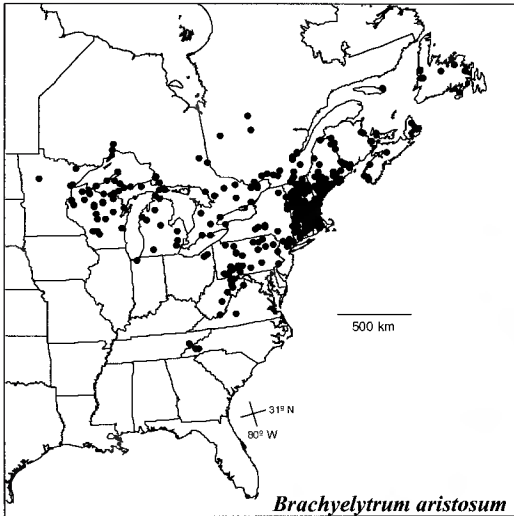


FIG. 4. Geographical distribution of *Brachyelytrum aristosum*.

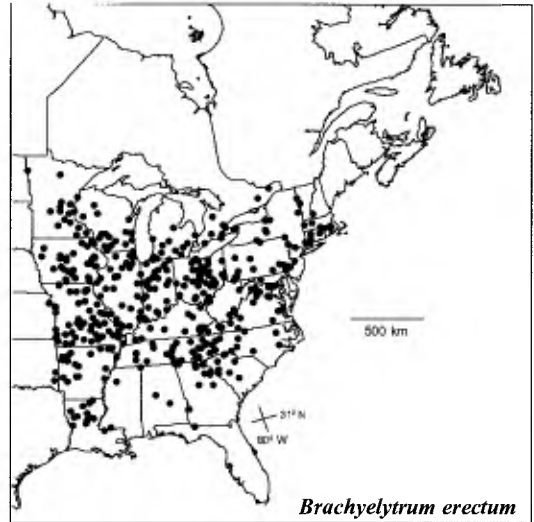


FIG. 5. Geographical distribution of *Brachyelytrum erectum*.

(–8.8) mm long] (Table 1). *Brachyelytrum japonicum* tends to be the smallest of the three species, with shorter spikelets, shorter awns, and fewer spikelets per panicle than North American plants (Table 1). The surface morphology of the lemma in *B. japonicum* is very similar to that of *B. aristosum*, with very small scaberulous hairs whose maximum length ranges from 0.1–0.2 mm (Table 1) distributed both on and between the lemma veins (Fig. 3).

Phytogeography. *Brachyelytrum erectum* and *B. aristosum* have unique but somewhat overlapping ranges in eastern North America. *Brachyelytrum aristosum* has a smaller, more northerly distribution, occurring from northern Minnesota south to northern Indiana, west to Pennsylvania, north to Newfoundland and west to southern Quebec, and southern Ontario (Fig. 4). The range of the species also extends south through the Appalachian Mountains in West Virginia, southwestern Virginia, southwestern North Carolina, and eastern Tennessee. *Brachyelytrum aristosum* is sympatric with *B. erectum* in the northeastern United States and south through the Appalachian mountains. The physiographic provinces in which *B. aristosum* is most common are the north-eastern Central Lowlands, the southeastern Canadian Shield, New England-Maritime Provinces, the northern half of the Blue Ridge Province, and the Ridge and Valley Province (Brouillet and Whetstone 1993).

Brachyelytrum erectum is the most widespread species in the genus. It occurs from northwestern Minnesota south to northern Louisiana, east to the northern tip of Florida, and north to Massachusetts, northeastern New York, and southern Ontario (Fig. 5). Its range occupies several of the physiographic provinces in eastern North America, and is most common in the eastern

Central Lowlands, Appalachian Highlands (including Appalachian Plateaus Province, Ridge and Valley Province, Blue Ridge Province, Piedmont Plateau Province, Interior Low Plateaus Province, Ozark Plateaus Province, and Ouachita Mountains Province) and the northern part of the southern Coastal Plain (Brouillet and Whetstone 1993).

Brachyelytrum japonicum is endemic to eastern Asia and is known from throughout central and southwestern Japan, the southern Korea island of Quelpart, and in eastern China in the provinces of Anhui, Jiangsu, Jiangxi, Yunnan, and Zhejiang (Fig. 6).

AFLPs. A total of 90 bands were scored for the five AFLP markers used in this study, with 52 (58%) being monomorphic and 38 (42%) polymorphic. Two types of polymorphic bands were observed: those that varied

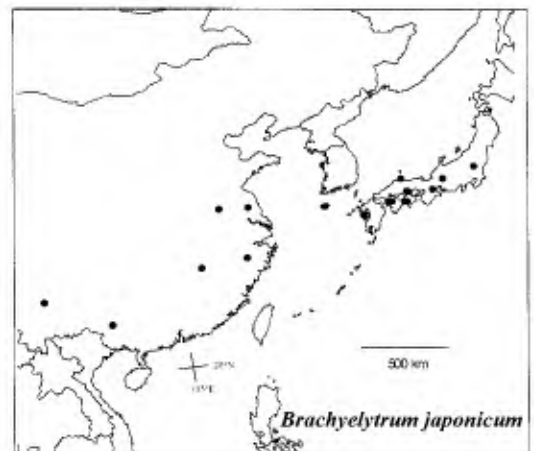


FIG. 6. Geographical distribution of *Brachyelytrum japonicum*.

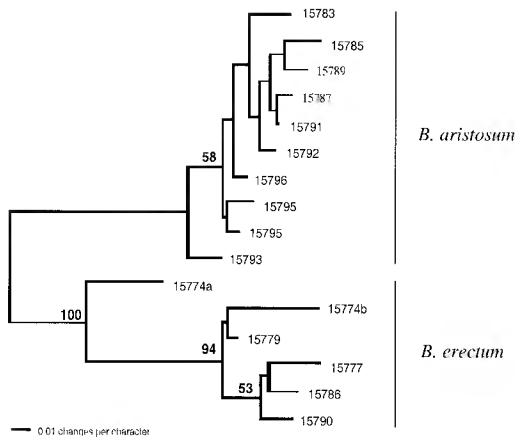


FIG. 7. Genetic relationships among 16 populations of *Brachyelytrum* (10 *B. aristosum*; 6 *B. erectum*) inferred from analysis of AFLP markers. Each population is represented by one individual. Numbers above branches represent bootstrap support values.

within a species and those that varied between species. Bands ranged in size from 50 to 300 base pairs. There were many more bands produced by these primer combinations that were not used in the analysis due to difficulty or ambiguity of scoring. The Minimum-Evolution dendrogram separated the North American plants into two well-supported (BV = 100) groups: one corresponding to individuals of *B. aristosum* and the other to individuals of *B. erectum* (Fig. 7). One individual of *B. erectum* (15774a) appeared to be somewhat genetically distinct from other individuals of *B. erectum*. The primer combinations used yielded several unique species-specific bands that clearly distinguish each of the North American species. Within a species, relationships among individuals were completely resolved but poorly supported (BV < 50).

Ecology. When plants were collected in the field we noted local conditions and vascular plant associates. In the range of sympatry, we observed populations of both species growing as little as one mile apart, but found no mixed populations or intermediate specimens. While we did not conduct any detailed ecological analyses, we were unable to discern any obvious differences in ecological preference between *B. erectum* and *B. aristosum*. We observed both species growing in varied habitats from flat ground in shaded moist woods, steep slopes (often with rocky substrates) along roadsides on the forest edge, and in fairly disturbed forest edges. The following taxa, listed in descending order of occurrence, were found associated with *B. erectum* and *B. aristosum* (nomenclature follows Gleason and Cronquist 1991): *Acer* spp., *Quercus* spp., *Leersia virginica*, *Muhlenbergia tenuiflora*, *Actaea alba*, *Pilea pumila*, *Polystichum acrostichoides*, *Impatiens* sp., *Betula* sp., *Prunus serotina*, *Pteridium aquilinum*, *Osmunda*

spp., *Festuca subverticillata*, *Tsuga canadensis*, *Elymus hirsutus*, *Danthonia spicata*, *Adiantum* spp., *Bromus pubescens*, *Thalictrum* spp., *Muhlenbergia sobolifera*, *Viola* spp., *Juncus* sp., *Microstegium viminium*, *Tilia* sp., *Fragaria* sp., *Panicum (Dichanthelium)* sp., *Glyceria* sp., *Crataegus* sp., *Smilacina* sp., *Rubus* sp., *Ahus* sp., *Potentilla* sp., *Ribes* sp., *Campanula americanum*, *Aralia* sp., *Oxalis* sp., *Fraxinus* sp., *Vitis* sp., and *Clethra acuminata*.

DISCUSSION

Morphological characteristics can be used to easily distinguish three distinct morphological entities in *Brachyelytrum*. The discriminant analysis was able to clearly separate all three species and classified 99% of the individuals successfully. The PCA visually displayed the morphological variability in the genus and showed that each of the taxa in *Brachyelytrum* differs in its overall size. There was some overlap between species in the PCA that can be attributable to the continuous and overlapping ranges in many of the characters that are not particularly useful in delineating taxa, and suggests a high degree of overall morphological similarity among taxa. The degree of difference exhibited in the PCA among the species of *Brachyelytrum* is similar to that found between other closely related species in several recent studies (e.g. Allen 2001; Rothrock and Reznicek 2001; Peterson et al. 2002).

Plotting the geographic locations of collection records of *Brachyelytrum* on maps showed that all three species have unique geographical distributions (Figs. 4–6). While the ranges of the North American species are somewhat overlapping, mixed populations were not observed in this study, nor by Stephenson (1971) who observed both taxa growing close together in Michigan but never mixed. No herbarium sheets containing more than one species were encountered. Developmental and phenological differences between the two species of *Brachyelytrum* in Michigan were observed by Stephenson (1971), who found that the northern taxon (= *B. aristosum*) exhibited more rapid growth and underwent anthesis 8 to 10 days sooner than did the southern taxon (= *B. erectum*). He suggested that these phenotypes are genetically controlled and that they are useful in differentiating the two taxa. Our AFLP data provide further evidence that there are two genetically distinct groups in *Brachyelytrum* in North America that correspond with the morphologically distinct entities detected by the multivariate analyses. We did not quantify levels of genetic variation within and between North American species, but the fact that one individual of *B. erectum* appeared highly genetically distinct from other individuals of this species warrants further investigation into patterns and levels of genetic variability.

These various lines of evidence from morphology, phytogeography, and AFLPs suggest that North Amer-

ican *Brachyelytrum* comprise two distinct evolutionary lineages that are best recognized as distinct species. While no molecular data are currently available for the Asian taxon, it is morphologically and phytogeographically distinct and therefore also best recognized as a distinct species.

The type specimen of *B. erectum* in the multivariate analyses appears to be morphologically similar to specimens of *B. aristosum* (Fig. 2). On this specimen, the length of the longest hairs on the lemma is 0.3 mm, which falls outside the average range of variation observed for this character (mean \pm one s.d.) in *B. erectum*, but is not outside the limits of observed variation when outliers are included (Table 1). In addition, the measurement clearly falls outside the range of variation observed in all specimens of *B. aristosum* (Table 1) and when all of the combined morphological characters were taken into account this specimen was classified in the DA as belonging to *B. erectum*. Clearly the type specimen is not an ideal representation of the species, but this is acceptable from a nomenclatural point of view as Article 7.2 of the International Code of Botanical Nomenclature (Greuter et al. 2000) states that "the nomenclatural type is not necessarily the most typical or representative element of a taxon."

A small number of apparently intermediate specimens thought to be hybrids have been reported from Michigan (Stephenson 1971) and New York (Tucker 1988), but when the main diagnostic character of lemma hair length is used to distinguish the North American species, we were not able to discern any intermediate specimens. However, one specimen of *B. erectum* was misclassified in the DA and had an intermediate position in the ordination space, suggesting that it may have been of hybrid origin. We initially hypothesized that plants with long spike pubescence and dense inter-nerve pubescence were intermediate in nature (following Stephenson 1971), but it became clear that the distribution of hairs between the lemma veins was simply variable in *B. erectum*. Past concepts of intermediate specimens were probably based on incomplete knowledge of the range of variation in taxonomically informative characters for the species but the possibility of hybridization in the genus cannot be discounted without further evidence.

Brachyelytrum is one of approximately 65 genera that exhibits the eastern North American and eastern Asian disjunct distribution pattern (Wen 1999). This classic intercontinental disjunction has interested botanists for over a century (e.g. Gray 1846; Li 1952; Boufford and Sponberg 1983; Wen 1999) and has been documented in other groups of organisms, including insects (e.g. von Dohlen et al. 2002) and fungi (e.g. Wu et al. 2000). This floristic disjunction has resulted from fragmentation and range restriction of a widespread mesophytic forest during the Tertiary that attained its in-

tercontinental distribution via the Bering and North Atlantic land bridges (e.g. Manchester 1999, reviewed in Wen 1999, 2001). Tiffney (1985a, b) reviewed the fossil, climatic, and geologic evidence and hypothesized multiple origins of the eastern North American and eastern Asian disjunct pattern. He proposed five periods during the Tertiary (pre-Tertiary, early Eocene, late Eocene-Oligocene, Miocene, and late Tertiary-Quaternary) during which migration of the disjunct genera across the Bering and North Atlantic land bridges probably occurred. Molecular data offer independent support for the multiple origins of the disjunction pattern (e.g. Lee et al. 1996; Wen et al. 1996; Xiang et al. 1998). Following this scenario, it is likely that *Brachyelytrum* attained its current intercontinental distribution during the Miocene period when the climate was such that only temperate deciduous plants were able to migrate (Tiffney 1985a). Though the North American and Asian species diverged several million years ago, it is unknown which of the two North America taxa *B. japonicum* is more closely related to. However, since *Brachyelytrum* is comprised of only three species, resolution of phylogenetic relationships in the genus should be relatively easy. Interestingly, phylogenetic studies on larger disjunct genera have revealed that presumed intercontinental species pairs are usually not closely related but have undergone further diversification following the initial divergence (e.g. Wen and Shi 1999; Gould and Donoghue 2000; Li et al. 2000; Wen 2000; Whitcher and Wen 2001; reviewed in Wen 1999, 2001).

Within North America, the current distribution of *Brachyelytrum* has been shaped by past climatic and geologic changes. Pohl (1978) noted that the distributions of the North American taxa closely correspond with glacial limits in eastern North America (see Flint 1971). The range of *B. erectum* occurs primarily south of the glacial boundary and could have persisted through the last glacial period. The majority of the range of *B. aristosum* occurs north of the glacial boundary, thus this taxon may have survived the last glaciation in refugia, and/or in compressed zones of suitable habitat along the southern ice sheet boundary, and attained its current distribution through postglacial expansion. Populations of *B. aristosum* at higher altitudes in the Appalachian Mountains south of the glacial boundary may represent such glacial refugia. Alternatively, these southern populations may be the result of southern migration into high altitude areas where climatic conditions are presumably more comparable with those found in the northern portion of its range.

The species in *Brachyelytrum* are clearly distinct but all three maintain high degrees of morphological similarity (Fig. 2). Despite a divergence that may have occurred as early as the Miocene, it appears that not a lot of subsequent morphological change has occurred in the evolutionary lineages found in North America

and Asia. This lack of morphological change has been observed in several other congeneric eastern North America and eastern Asia disjunct species (e.g. Wen 2000), and has been referred to as morphological stasis, or the lack of character evolution over a long period of time (reviewed in Wen 2001). Despite the high degree of morphological similarity, these disjunct taxa often exhibit high levels of molecular divergence corresponding to a long period of isolation (e.g. Parks and Wendel 1990). The level of molecular divergence among Asian and North American species of *Brachyelytrum* is currently unknown, but appears to be high among the North American species.

This taxonomic revision of *Brachyelytrum* provides a solid framework for further evolutionary studies in the genus. Information on levels of molecular divergence in species of *Brachyelytrum* has considerable potential to provide further insight into the time of the initial intercontinental divergence of species in the genus and resolution of phylogenetic relationships. Further research on patterns and levels of genetic diversity in the species of *Brachyelytrum* may shed light on the localities of potential glacial refugia and patterns of post-glacial dispersal (see Comes and Kadereit 1998), provide insight into levels of gene flow within and between populations, and possibly identify potential hybrid populations.

Detailed taxonomic monographs and morphological studies exist for only a few eastern North American and eastern Asian disjunct genera, including *Boykinia* Nutt. (Gornall and Bohm 1985), *Diphylleia* Michx. (Ying et al. 1984), *Pachysandra* Michx. (Boufford and Xiang 1992), and *Campsis* Lour (Wen and Jansen 1995). Two other eastern North American and eastern Asian disjunct grass genera, *Diarrhena* P. Beauv. (if *Neomolina* Honda is included) and *Zizania* L., have both been the subjects of recent taxonomic revisions but neither of these studies included the Asian congeners (Brandenburg et al. 1991; Terrell et al. 1997). *Osmorhiza* Raf. is an excellent example of a disjunct genus for which complete monographic and phylogenetic data exist (Lowry and Jones 1984; Wen et al. 2002; Yoo et al. 2002). Future studies comparing patterns of both morphological and molecular variation in eastern North American and eastern Asian disjunct genera will be critical to further understanding this classic phytogeographic pattern.

TAXONOMIC TREATMENT

BRACHYELYTRUM P. Beauv., Ess. Agrostogr. 39, 155. 1812. TYPE: *Brachyelytrum erectum* (Schreb.) P. Beauv.

Herbaceous perennials. Rhizomes short-prostrate, knotty, covered with cataphylls; cataphylls 0.2–0.8 mm long, ca. 0.2 mm wide, ovate-lanceolate, apically rounded, acuminate or acute, brownish white, glabrous. Shoot cataphylls light brown, linear-lanceolate, apically acute, abaxially scaberulous, adaxially pilose, margins sometimes chartaceous. Culms erect, unbranched, terete, glabrous to pubescent; internodes solid, glabrous or pubescent. Sheaths tightly surrounding culm, margins overlapping, collar visible, yellow-beige to white, glabrous to hispid. Ligules membranous, entire or ciliate, yellow-white. Leaf blades linear-lanceolate to narrowly lanceolate-oblong, constricted at base, apically acute or acuminate, pubescent on surface and margins, distinctly veined; sheaths terete, margins open. Inflorescence a narrow contracted panicle with few to several appressed branches, erect to nodding or reflexed to appressed, essentially glabrous, few to several spikelets. Spikelets dorsally compressed, solitary, pedicellate; pedicels dilated below spikelet, 0.5–0.8 mm long, minutely scabrous; 1-flowered, disarticulating above the glumes; rachilla cylindrical, antrorsely scabrous, whitish green with small apical rudiment ca. 0.1 mm long. Glumes reduced, unequal, glabrous or scabrous, apically acuminate to acute; lower glume sometimes highly vestigial but never obsolete, \pm 1-veined, scale-like, shorter than upper glume, dark green \pm hyaline margins or entirely hyaline; upper glume subulate to lanceolate, shorter than floret, 1-veined, hyaline margins. Florets 1; lemma herbaceous, tightly enveloping the palea, 5-veined, terete, distal margins involute, lower 1/3 of margin chartaceous, tapering to a single awn; awn longer than body of lemma, straight, antrorsely scabrous; callus ca. 0.8 mm long, pilose, brownish-yellow; palea 2-veined, awnless, glabrous, scabrous or hispid, same length as lemma, light green, sometimes with a bifid apex; lodicules 2. Stamens 3, anthers yellow, broader than filament. Stigmas 2, white, feathery. Caryopsis narrowly oblong-elliptic with a vertical groove on one side, tip with narrow, hairy beak. Base chromosome number of $x = 11$. Three species: two in eastern United States and Canada, one in eastern Asia.

KEY TO THE SPECIES OF BRACHYELYTRUM

1. Widest leaf blades 0.5–0.7 (–0.8) cm wide; rachilla (6.8–) 7.2–8.4 (–8.8) mm long; lower glume (0.2–) 0.4–1.6 (–2.0) mm long; plants from Asia *B. japonicum*
1. Widest leaf blades 0.8–2.0 cm wide; rachilla (3.9–) 4.9–7.2 (–8.1) mm long; lower glume (0.1–) 0.2–0.7 (–1.1) mm long; plants from North America 2
 2. Lemma (0.7–) 0.8–1.2 (–1.4) mm wide, minutely scabrous, longest hairs (0.06–) 0.08–0.14 (–0.2) mm long, not evident under

10× magnification, weakly veined, mid-vein like secondary veins; widest leaf blade (0.8–) 1.0–1.4 (–1.6) cm wide

- *B. aristosum*
 3. Lemma (0.8–) 1.1–1.5 (–1.8) mm wide, hispid, longest hairs (0.2–) 0.4–0.8 (–0.9) mm long, easily seen under 10× magnification, conspicuously veined, mid-vein highly prominent; widest leaf blade (0.9–) 1.1–1.7 (–2.0) cm wide *B. erectum*

1. *BRACHYELYTRUM ARISTOSUM* (Michx.) Trel. in Branner and Coville, Annual Rep. Arkansas Geol. Surv. 1888(4): 235. 1888 [1891] Basionym: *Dilepyrum aristosum* Michx. Figs. 3b, 4.

NOTE: as "*B. aristosum*"; comb. erroneously attributed to P. Beauv. by Trelese, in Branner and Coville. Branner and Coville, the main authors of the report, clearly indicate that Trelese was responsible for the nomenclature in their publication.

Dilepyrum aristosum Michx., Fl. Bor.-Amer. 1: 40. 1803. T-Protol.: Hab. in umbrosis sylvis Georgiae et Carolinae. T-Specim.: USA: In umbrosis Carolinae sylvis [LT (here designated): P (herb. A. Richard) (fide: J. Cayouette 2001!; also from digital image RJS & PMP!; ILT: US-865848!* (fragm. ex "herb. Pitt and Dur., ex herb. Richard"))].

NOTE: The original distribution of the species was given as Georgiae and Carolinae. However, there are no specimens in the Michaux herbarium (P) under this species or its synonyms, and there is only one specimen in the A. Richard herbarium (P), and that is from "Carolinae". Richard described many of Michaux's new taxa (fide: TL-2), and many types not present in the Michaux herbarium are present in the Richard herbarium. A. S. Hitchcock annotated the US type fragment as "type or duplicate type", "herb. Pitt. and Dur. [BR] ex herb. Richard". Agnes Chase (1937, Am. J. Bot. 24(1): p. 33) explains that in 1935, Hitchcock found this specimen, which was missing from P, in the Brussels herbarium. She concluded that its presence in Brussels was "doubtless due to the mistake of some assistant in the Paris Herbarium many years ago, in sending out duplicates or in returning loans". The *Dilepyrum* specimen was apparently returned to P, and is the only extant original Michaux collection of the species of which we are aware. Today there are no Michaux specimens in the Pittier and Dureau special collection, nor in other collections at BR (fide Elmar Robbrecht, BR, 2001.). It is possible that there exists or did exist a Michaux collection from "Georgiae". We designate the "Carolinae" specimen as a lectotype, though it may in fact represent the holotype.

Muhlenbergia aristata Pers., Syn. Pl. 1: 73. 1805.

NOTE: nom. illeg. superfl., as "*aristata*", an illegitimate renaming of *Dilepyrum aristosum* Michx. "*Aristosum*" is etymologically correct Latin and means abundantly awned (fide D. Nicolson, US, 2001). Persoon did not cite the binomial itself, but his intent was clear enough, as he cited the original description of that and gave "Richard, Michaux"

for authors, and also placed *Dilepyrum* in synonymy with *Muhlenbergia* in the index (p. 532).

Brachyelytrum aristatum P. Beauv. ex Roem. and Schult., Syst. Veg. 2: 413. 1817.

NOTE: nom. illeg. superfl., as "*Brachyelytrum aristatum* P. Beauv." This is a second illegitimate renaming of *Dilepyrum aristosum* Michx., following Persoon (1805) in the spelling of the specific epithet. The name was not effectively established by Palisot de Beauvois (*Ess. Agrostogr.* 1812), where the species name is cited under, but not combined with, *Brachyelytrum*.

Brachyelytrum aristatum P. Beauv. ex Trel. in Branner and Coville, Annual Rep. Arkansas Geol. Surv. 1888(4): 235. 1888 [1891].

NOTE: nom. inval., comb. not made by Palisot de Beauvois (ibid.). This name is listed as a synonym of *Brachyelytrum aristosum*. Branner and Coville as the authors of the report are often cited as the authors of the nomenclatural innovations in the report. However, it is clearly indicated in the report that Trelese did the nomenclatural research, and as such the nomenclatural innovations should be attributed to him.

Brachyelytrum aristosum (Michx.) Trel. var. *aristosum* (autonym; autonym generator, *B. aristosum* var. *glabratum* Vasey, 1892)

Brachyelytrum erectum var. *septentrionale* Babel, Rhodora 45(534): 260. 1943. T-Protol.: USA: New Hampshire: Strafford Co.: Durham, rich soil in open woods near Horticultural Farm, 19 Jun 1942, *Babel* 46 [HT: WIS!]. T-Specim.: 1 of 1. USA: New Hampshire: Strafford Co., 19 Jun 1942, *W.K. Babel* 46 [HT: WIS!; IT: F, GH, US-1867524!*].

Brachyelytrum septentrionale (Babel) G.C. Tucker, J. Arnold Arbor. 69(3): 253. 1988. Basionym: *Brachyelytrum erectum* var. *septentrionale* Babel.

Culms (28.5–) 41–78 (–96) cm tall, 0.6–1.0 mm wide at mid-culm; internodes (3.9–) 5.4–11.4 (–15.5) cm long, glabrous, slightly hispid to hispid; nodes densely pilose. Sheaths (3.2–) 4.5–7.8 (–10.4) cm long, pubescent. Ligules 1.8–2.5 mm long. Blades (6.9–) 8.6–13.0 (–16.1) cm long, (0.8–) 1–1.4 (–1.6) cm wide, linear-lanceolate, abaxially pilose on veins, adaxially somewhat pilose on veins; margins ± hyaline, scabrous with (1–) 8–19 (–23) prickle teeth per 2 mm of margin, and ciliate with (0–) 3–12 (–17) macrohairs per 2 mm of margin. Panicles (6.6–) 9.5–16.5 (–17.5) cm long, 0.4–0.8 cm wide with (0–) 2–5 (–7) branches. Spikelets (23–) 26–32.6 (–36) mm long including awns, (8–) 13–34 (–55) per panicle; rachilla (4–) 4.9–6.3 (–6.9) mm long.

Lower glume (0.1–) 0.2–0.4 (–0.9) mm long; upper glume (0.6–) 0.7–1.7 (–3) mm long. Lemmas (0.7–) 0.8–1.2 (–1.4) mm wide, veins equally prominent, white or green; callus pilose; veins densely scaberulous with hairs 0.08–0.14 (–0.2) mm long; awn (14–) 17–22.6 (–26) mm long. Paleas (7.7–) 8.4–10.4 (–11.5) mm long. Anthers 2.0–3.5 mm long. Caryopses 5.5–7.5 mm long, brown to dark brown.

COMMON NAMES. Northern short-husk; Bearded short-husk; Long-awned wood grass

Representative Specimens Examined. U.S.A. Connecticut: Fairfield Co., Greenwich, 9 Jul 1907, *Cushman 1142 & Sanford* (GH); Hartford Co., Southington, 26 Jun 1897, *Bissell s.n.* (GH*); Litchfield Co., Washington, 9 Jul 1919, *Evans s.n.* (GH); Middlesex Co., Had-dam, 4 Aug 1916, *Weatherby s.n.* (US, GH); New Haven Co., Milford, 22 Jul 1920, *Evans s.n.* (GH); New London Co., Franklin, 24 Jul 1911, *Woodward s.n.* (GH); Tolland Co., Andover, 7 Jul 1940, *Travis 2428* (US); Stafford Woods, Hedgehog Hill, 4 Jul 1991, *Mehrhoff 14685* (GH*); Windham Co., Central Village, 17 Jul 1901, *Sheldon 656* (GH*). Indiana: Porter Co., Keiser, 13 Jul 1924, *Lyon Jr. s.n.* (US). Maine: Aroostook Co., Monticello, 12 Jul 1916, *Fernald 12755 & Long* (GH*); Cumberland Co., Cape Elizabeth, Jul 1895, *Gayle 798* (US*); Hancock Co., Reach, Deer Isle, 6 Jul 1915, *Hill 2150* (GH*); Coon Bog Brook, Dedham, 18 Jul 1916, *Fernald 12611 & Long* (GH); Kennebec Co., Monks' Hill, Readfield, 14 Jul 1933, *Fernald s.n.* (GH); Knox Co., Camden, 11 Jul 1902, *Kennedy s.n.* (GH*); Lincoln Co., Jefferson, 27 Jul 1932, *Knowlton s.n.* (GH); Oxford Co., Snow Falls, near West Paris, 20 Jul 1938, *Palmer 44571* (GH); Penobscot Co., Orono, 14 Jul 1890, *Fernald s.n.* (GH*); Washington Co., Codyville, 8 Aug 1940, *Knowlton s.n.* (GH); York Co., Old Orchard Beach, 19 Jul 1968, *Wells s.n.* (GH). Maryland: Garrett Co., near Boiling Springs, vicinity of Oakland, 3 Aug 1950, *Allard 19743* (US). Massachusetts: Berkshire Co., Sheffield, 24 Jun 1919, *Churchill s.n.* (MO); Essex Co., Boxford, 21 Jun 1952, *Hunnewell 19795* (GH); Franklin Co., Bear River Creek, Conway, 18 Jun 1921, *Svenson s.n. & Hunnewell* (GH); Hampden Co., Granville, 26 Jun 1914, *Seymour 201* (MO); Worcester Co., 27 Jun 1897, *Greenman 3207* (MO); Worcester Co., Norfork, 22 Jun 1911, *Wiegand 1104* (GH); Berkshire Co., Bears Den Swamp, Sheffield, 24 Jun 1919, *Churchill s.n.* (GH); Bristol Co., Rattlesnake Brook, W of Bell Rock Road, Freetown, 14 Sep 1986, *Sorrie 3667* (GH); Essex Co., Brookwood Road, Beverly Farms, 23 Jun 1913, *Hubbard 589* (GH); Franklin Co., Shutesbury, 28 Jul 1930, *Seymour 3591* (GH); Hampden Co., Wales, 27 Jul 1941, *Hunnewell 17349* (GH); Hampshire Co., Univ. of Massachusetts campus, Amherst, 5 Jul 1967, *Ahles 67411* (US*); Prescott, 18 Jul 1929, *Goodale et al. 56997* (GH); Middlesex Co., Hopkinton, 5 Jul 1919, *Hunnewell 6003* (GH); Norfolk Co., Norwood, 27 Jun 1897, *Williams s.n.* (GH*); Suffolk Co., Happy Valley, Stony Brook Reserve, 17 Jun 1895, *n.c.* (GH); Worcester Co., Royalston, 3 Aug 1946, *Richardson 7287 & Seymour* (GH). Michigan: Alger Co., 13 Aug 1934, *Hermann s.n.* (MO); Cheboygan Co., Riggsville Fog 2.5 mi. SE of Douglas Lake, 20 Jul 1919, *Dean 28789* (US); Dickinson Co., near Floodwood, 4 Jul 1915, *Dodge s.n.* (US); Keweenaw Co., Meadows, 21 Jul 1889, *Farwell 561* (US); Marquette Co., Gwinn, 21 Jul 1907, *Harrison s.n.* (US*); Ontonagon Co., 22 Aug 1969, *Seymour 18271* (MO). Minnesota: Aiken Co., 15 Aug 1891, *Sandberg 838* (MO); Carlton Co., Jul 1889, *Woods s.n.* (US*); Clearwater Co., Itasca State Park, 27 Jul 1929, *Grant 2942* (US, GH); St. Louis Co., Loon River Echo Trail, Ely, 9 Jul 1939, *Barrows s.n.* (US). Missouri: Jackson Co., Dodson, 26 Sep 1897, *Bush 305* (US). New Hampshire: Belknap Co., Barnstead, 10 Jul 1964, *Rossbach s.n.* (GH, MO); Carroll Co., Pinkham Notch, Jackson, 14 Jul 1967, *Harris 31134* (GH); Cheshire Co., Alstead, 0.8 km N of the Surry-Alstead town line on New Hampshire route 12-A, 20 Aug 1974, *Boufford et al. 15596* (US); Coos Co., 4 mi. S of Lykens, alt. 1080 ft., 13 Jul 1952, *Berkheimer 14050* (GH); Grafton Co., SE corner of Mascoma Lake, 31 Jul 1932,

Bullard s.n. (GH); Hillsboro Co., Peterboro, 18 Jul 1937, *Knowlton s.n.* (GH); Merrimack Co., Hooksett, 6 Jul 1926, *Batchelder s.n.* (GH*); Rockingham Co., near Piscassic River, Newfields, 8 Oct 1920, *Harris 24011* (GH); Stafford Co., W of Bow Lake, 6 Sep 1950, *Hodgkin 6872* (GH); Sullivan Co., Buckhaven, 19 Aug 1897, *Weatherby s.n.* (GH). New Jersey: Mt. Tahor, Sep 1924, *Tate 10454* (GH*); Bergen Co., Bear Swamp, Culver's Gap, 4 Jul 1919, *Griscom 1542* (GH); Hunterdon Co., along Musconetcong River above Warren Glen, 4 Sep 1939, *Long 53898* (GH); Morris Co., 16 Jul 1905, *Mackenzie 1529* (MO); Passaic Co., Allwood Swamp, Clifton, 16 June 1935, *Yerbury 1763 & Clausen* (GH*). New York: Chenango Co., McDonough, 1 Jul 1884, *Coville s.n.* (US); Cortland Co., along Beaver Brook, Cortland, 19 Jul 1916, *Metcalf 5632* (GH, MO); Delaware Co., Griffins Corner, 13 Jul 1892, *Schrenk s.n.* (MO); Essex Co., Whiteface Mt. near Lake Placid, 17 Aug 1917, *Hitchcock 15984* (US); Hamilton Co., 16 Jul 1931, *Muenschner 1909 & Maguire* (MO); Orange Co., near Babcock Tr., Black Rock Forest, 30 Jun 1936, *Raup 7383* (GH*); Rockland Co., Bear Mountain State Park, 16 Jul 1939, *Moldenke 11190 & Moldenke* (US); Ulster Co., along Beaverkill River E of Turnwood, alt. 2500 ft., 8 Aug 1940, *Gleason 9938* (US); Washington Co., Sugar Loaf Mt., 5 Jul 1897, *Burnham s.n.* (GH*). North Carolina: Haywood Co., Black Mountain, on the Blue Ridge Parkway SW of its intersection with North Carolina route 215, 8 Sep 1974, *Boufford 15657* (GH); Jackson Co., Tuckaseeige Falls, 7 Jul 1931, *Blomquist 184* (US); Ohio: Portage Co., W of "Way Swamp", SW of Co. Rd. 210, Shalersville Twp., 29 Jun 1978, *Andreas 2132* (US). Pennsylvania: Centre Co., Black Moshannon Dam, 23 Jul 1950, *Westerfeld s.n.* (GH); Clearfield Co., Crystal Springs Camp, 13 Jul 1947, *Wahl 2955* (GH*); Elk Co., 3 mi. NW of Wilcox, 29 Jun 1940, *Wahl 774* (ISC, GH*); Fayette Co., Ohiopyle, 3 Jul 1905, *Ricker 1214* (US); Luzerne Co., 31 Jul 1926, *Heller s.n.* (MO); Lycoming Co., along Blockhouse Creek 2 mi. W of Buttonwood, alt. 370–470 m, 23 Jun 1939, *Fosberg 16563* (US); Monroe Co., Pocono Plateau, Jul-Aug 1904, *Harshberger s.n.* (US, GH); Sullivan Co., top of North Mountain, E of main E fork of Painters Run, alt. 750 m, 3 Sep 1938, *Fosberg 15869* (US); Warren Co., Sandstone Springs, 4 Jul 1945, *Moldenke 17599* (US). Rhode Island: Bristol Co., near Diamond Hill, 27 Jun 1942, *Palmer 46219* (GH). Vermont: Malingford, 28 Jul 1907, *Kennedy s.n.* (GH); Addison Co., Hancock, 7 Jul 1908, *Williams s.n.* (GH); Caledonia Co., near Groton L., Groton, 18 Jul 1960, *Seymour 18812* (GH, MO); Rutland Co., 31 Jul 1967, *Seymour 25765* (MO); Essex Co., Canaan, 21 Aug 1968, *Harris 33311* (GH); path to Unknown Pond, above Route 114, Warren Gore, 11 Jul 1981, *Zika 4121* (GH); Orange Co., along Orange Brook, Orange, 27 Jul 1960, *Seymour 19019* (US*); Orleans Co., Bartow, 16 Jul 1938, *Litch 54* (GH); Rutland Co., Long Trail, Mt. Tabor, 7 Aug 1966, *Seymour et al. 4438* (GH); Washington Co., Middlesex, 9 Jul 1942, *Knowlton s.n.* (GH); Windham Co., Brattleboro, 19 Jun 1925, *Churchill s.n. & Knowlton* (GH*); Halifax, 21 Jun 1925, *Knowlton s.n.* (GH*); Windsor Co., Quechee Gulf, 15 Jul 1881, *Leland s.n.* (GH). Virginia: Bedford Co., 10 Jul 1871, *Curtis 9282* (MO); Giles Co., 28 Jun 1950, *Shanks 15299* (GH). West Virginia: Randolph Co., along Cheat River, Cheat Mountain, near Cheat Bridge, 9 Jul 1942, *Hutton s.n.* (GH); Tucker Co., Brown Mt., 8 mi. E of Davis, Canaan Valley, alt. 900–1200 m., 2 Jul 1939, *Allard 6883* (US). Wisconsin: Forest Co., 6 mi. W of Armstrong Creek, 21 Jul 1926, *Ball 2422* (ISC, US); Lincoln Co., valley of the Wisconsin River near Noisy Creek, 1893, *Cheney 1895* (US); Sauk Co., 15 Jul 1903, *Eggert s.n.* (MO), Pine Hollow Area, Devil's Lake State Park, 29 Jun 1958, *Hartley 4247* (US*); Wood Co., Pittsville, 25 Jul 1927, *Colby 4449* (US).

CANADA. Newfoundland: near Winterhouse Brook, Bonne Bay, 8 Aug 1929, *Fernald et al. 1329* (US**); banks of Badger Brook near its confluence with the Exploits River, 13 Aug 1894, *Robinson 197 & Schrenk* (MO, US*); Benoit's Cove, 23 Aug 1910, *Fernald et al. 2494* (GH, US); near mouth of Main River, 27 Aug 1929, *Fernald 1330 & Long* (US); Indian Bridge, Jul 1921, *Ayre s.n.* (GH); Beechan junction, 13 Jul 1930, *Jaussan s.n.* (GH, US); Bonne Bay, 27 Aug 1910, *Fernald et al. 2493* (GH). New Brunswick: Charlotte Co., Gib-

son, Showshoe & Welsh Lake vicinity, ca. 8 mi. NW of St. Andrews, 24 Jul 1929, *Malte* 56129 (GH); Kent Co., Carleton Parish, 5 mi. N along Hwy. 117 to Black River, 1 mi. W along river, Kouchibouguac National Park, 26 Jul 1978, *Munro* 2050 (GH*); Westmorland Co., Shediac Cape, 14 Jul 1914, *Hubbard* 704 (GH, US*). Nova Scotia. Middle Windsor road, 4 Sep 1947, *Swallen* 9927 (US); Annapolis Co., Young's Lake, North Mt., Belle Island, 19 Jul 1921, *Fernald et al.* 23248 (GH); Cape Breton Co., Warren Lake, Ingonish, Cape Breton, 9 Aug 1904, *Churchill s.n.* (GH); Digby Co., Meteghan, 7 Jul 1920, *Fernald 19868 & Long* (GH); Hants Co., along Five-Mile River, 19 Jul 1920, *Pease 19870 & Long* (GH); Victoria Co., Port Bevis, 27 Aug 1920, *Fernald 19873 & Long* (GH); Yarmouth Co., Belleville, 27 Jul 1920, *Long 19872 & Linder* (GH). Ontario: Algoma Co., Corbeil Pt., 5 Aug 1935, *Taylor et al.* 973 (US); Carleton Co., Osgood Twp., 3.8 km N of Osgood, 19 Jul 1992, *Darbyshire* 4431 (US*); Frontenac Co., Kingston, 21 Jul 1881, *Fowler s.n.* (US); Hastings Co., Mallingsford, 28 Jul 1907, *Kennedy s.n.* (GH*); Lanarck Co., Almonte, 6 Jul 1898, *Fowler s.n.* (US*); Muskoka Co., Lake of Bays, Muskoka, 8 Aug 1904, *Herriot* 6 (US); Parry Sound Co., Georgian Bay Islands, 14 Aug 1942, *McDonald* 462 (US). Quebec: Baie du Renard, 6 Aug 1925, *Marie-Victorin et al.* 20552 (US, GH*); Bolton, 25 Jul 1926, *Knowlton s.n.* (US*); Riviere du Renard, 6 Aug 1927, *Marie-Victorin 28063 & Rolland-Germain* (US*, GH); Swift Current, Pipers Hole River Bridge, 25 Jul 1960, *Rouleau* 5752 (US*); Sainte-Foy Co., Longeway's Falls, Sutton, 22 Aug 1916, *Edmondson* 5458 (GH); Carleton Co., King's Mt., 18 mi. N of Ottawa, 29 Jun 1938, *Carnes* 72 (US); Chelsea Co., Lake McGregor, vicinity of Ottawa, 3 Aug 1917, *Rolland 6061* (MO, US); Matane Co., Mt. Nicolabert, Joffre, 20 Jul 1922, *Fernald & Pease 24847* (GH*); Megantic Co., Caribou Hill, Black Lake, 29 Aug 1915, *Fernald 12006 & Jackson* (GH); Montcalm Co., Monroe Lake, Park du Mont Tremblant, 14 Jul 1957, *Rolland-Germain 368* (GH, US); Portneuf Co., Lac St-Joseph, 6 Jul 1941, *Rouleau 1044, Marie-Victorin & Rolland-Germain* (US, GH); Richmond Co., Cleveland, 26 Jul 1923, *Chamberlain & Knowlton s.n.* (GH); Sherbrooke Co., Lake Park Orford (?), 22 Jun 1923, *Knowlton s.n.* (GH*); Terrebonne Co., Saint Jerome, 22 Jul 1946, *Rolland-Germain 6080* (US*, GH*, MO).

2. BRACHYELYTRUM ERECTUM (Schreb.) P. Beauv., Ess. Agrostogr. 39, 155. 1812. Basionym: *Muhlenbergia erecta* Schreb. Figs. 3a, 5.

Muhlenbergia erecta Muhl., Trans. Amer. Philos. Soc. 3: 160. 1793. NOTE: nom. nud.

Muhlenbergia erecta Schreb., in Roth, Neue Beytr. Bot. 1: 97. 1802. T-Protol.: North America: "Habitat in America Boreali". T-Specim.: 1 of 1. USA: "Americk. sept. Pennsylvania (Lancaster?)", Communicavit Mühlenberg [HT: M (we here consider this to be the holotype); IT: PH (nos. 89 and 277 on one sheet)! (no. 277 is probably the isotype, as a remark in Mühlenberg's hand about the pubescent sheaths corresponds to Schreber's illustration (pl. 73, 1810), and no. 89 has nearly smooth sheaths)].

NOTE: We were unable to locate any specimens of the species at Erlangan (ER; *vide* W. Nezadal, pers. com. 2001) where Schreber worked for many years. Today his herbarium and types are at M (*vide* TL-2) and there is one original specimen of the species there. "We have here [M] a sheet (*Herbarium Schreberianum*) which was determined by Hitchcock (1922) and by Tucker (1988) as *Brachyelytrum erectum* (Schreb.) Beauv. and is kept in our

herbarium under this name. The Schreber collection is more or less completely here at M. This sheet has been originally unnamed. The label shows the following text: Americk. sept. Pennsylvania (Lancaster?) Communicavit Mühlenberg. The sheet has never been designated as type of *Muhlenbergia erecta* Schreb. but it seems to me to be the type. There is no sheet under *Muhlenbergia erecta*, *Agrostis erecta* or *Dilepyrum erectum*" (Wolfgang Lippert, M, pers. com. 2001).

Muhlenbergia erecta Schreb., Mem. Acad. Imp. Sci. St. Petersburg Hist. Acad. 2: 287. 1807–1808. T-Protol.: USA: "Habitat in Sylvis umbrosis Georgiae et Carolinae americanae".

NOTE: isonym; Chase and Niles's *Index to Grass Species* gives the publication date as 1807–1808, but this is likely in error as the journal series starts in 1809. It was also given in Schreber's *Beschr. Gräs.* 2: 139–141, pl. 73 (1810). Schreber, by this point in time, probably considered *Dilepyrum aristosum* Michx. to be synonymous with his species. Plate 73 is clearly identifiable as *B. erectum* and not *B. aristosum*.

Muhlenbergia brachyelytrum Trin., Gram. Unifl. Sesquifl. 188, 296, t. 5, f. 1. 1824.

NOTE: nom. superfl. illeg.; as "*Mühlenbergia Brachyelytrum*"; based on "*Brachyelytrum erectum* P. Beauv." [ex Roem. and Schultes; which is in turn based on *M. erecta* Schreb.]

Agrostis erecta (Schreb.) Spreng., Syst. Veg. 1: 264. 1825. Basionym: *Muhlenbergia erecta* Schreb.

Dilepyrum erectum (Schreb.) Farw., Amer. Midl. Naturalist 8: 33. 1922. Basionym: *Muhlenbergia erecta* Schreb.

Brachyelytrum erectum A. Gray subsp. *erectum* (autonym; autonym generator, *B. erectum* subsp. *japonicum* (Hack.) T. Koyama & Kawano, 1964)

Brachyelytrum erectum (Schreb.) P. Beauv. var. *erectum* (autonym; autonym generator, *B. erectum* var. *japonicum* Hack., 1899).

Brachyelytrum aristatum var. *engelmannii* A. Gray, Manual (ed. 5) 614. 1867. T-Protol.: USA: "A western form". T-Specim.: 1 of 1. Missouri: St. Louis [HT: GH (*vide* Babel 1943; "var. *engelmannii*" in Gray's hand according to Fernald; the specimen apparently lost); LT (here designated): MO-Engelmann herb., Belleville, Ill., Aug 1833, *Engelmann* 97. 140!].

NOTE: as "*B. aristatum*." The GH specimen mentioned by Babel has not been found in searches of GH collections (*vide* K. Gandhi and W. Kittredge 2001), and we conclude that it has been lost. G. Davidse has identified five *Brachyelytrum* specimens at MO in the Engelmann herbarium, only two of which have labels saying "George Engelmann, St. Louis Missouri". Of the latter two, one was collected by

Chr. A. Geyer in 1842, in Beardstown, Illinois. The other was collected by Engelmann, and has the following data, perhaps in his hand, "97. 140 shady woods, near Belleville, Ill.," with the date of August 1833. This matches Gray's description and we assume it to be a duplicate of the specimen Gray had in hand. We designate this as the lectotype.

Brachyelytrum aristosum var. *glabratum* Vasey, Bull. West Virginia Agric. Exp. Sta. 24: 469. 1892. T-Protol.: USA: West Virginia: near Nuttallburg; high, rocky woods, *L. W. Nuttall*. T-Specim.: 1 of 1. USA: West Virginia, Fayette Co., Nuttallburg, 1890, *L. W. Nuttall s.n.* [HT: F-100250; US-photostat of F-100250]. NOTE: as "*aristosum*"; isonym in Publ. Field Columbian Mus., Bot. Ser. 1: 194. 1896.

Brachyelytrum crectum var. *glabratum* (Vasey) T. Koyama and Kawano, Can. J. Bot. 42: 866. 1964. Basionym: *Brachyelytrum aristosum* var. *glabratum* Vasey.

Culms (34.5–) 44.4–71.4 (–102) cm tall, 0.6–1.0 mm wide at mid-culm; internodes (3.5–) 4.3–8.3 (–12.3) cm long, glabrous, slightly hispid to hispid; nodes densely pilose. Sheaths (3.1–) 4.1–6.1 (–7.2) cm long, hispid. Ligules 2.0–3.5 mm long. Blades (9.5–) 10.0–14.8 (–17.5) cm long, (0.9–) 1.1–1.7 (–2.0) cm wide, linear-lanceolate, abaxially pilose on veins, adaxially glabrous to slightly hispid, margins \pm hyaline, scabrous with (5–) 10–22 (–27) prickle hairs per 2 mm of margin and ciliate with 0–4 (–27) macrohairs per 2 mm of margin. Panicles (5.5–) 9.1–14.3 (–18.5) cm long, 0.4–0.8 cm wide, (0–) 1–4 (–6) branches. Spikelets (25–) 29.1–36.1 (–42) mm long including awns, (4–) 11–25 (–35) per panicle; rachilla (3.9–) 5.4–7.2 (–8.1) mm long. Lower glumes (0.1–) 0.3–0.7 (1.1) mm long; upper glumes (0.2–) 0.9–3.5 (–7) mm long. Lemmas (0.8–) 1.1–1.5 (–1.8) mm wide, mid-vein much more prominent than other veins, white, remaining veins white or green, callus pilose; veins hispid with hairs (0.2–) 0.4–0.8 (–0.9) mm long, interveinal surface glabrous, scaberulous, scabrous, or hispid; awn (14.3–) 19–27 (–32.4) mm long. Paleas (7.1–) 8.2–10.4 (–11.9) mm long. Anthers 3.3–6 mm long. Caryopses 5.5–7.5 mm long.

COMMON NAMES. Bearded short-husk; Long-awned wood grass.

Representative Specimens Examined. U.S.A. Alabama: Lee Co., Auburn, 18 Aug 1898, *Svenson 10355* (MO); Montgomery Co., Montgomery, May 1868, *Mohr s.n.* (US). Arkansas: Cross Co., Crowleys Ridge, Levesque P.O., alt. 260 ft., 24 Jul 1939, *Denaree 19614* (MO, US); Garland Co., Indian Mt., Hot Springs, 15 Aug 1937, *Scully 998* (US); Lawrence Co., Methodist Camp, Imboden P.O., elev. 300 ft., 25 Jun 1950, *Denaree 29229* (US); Stone Co., Caney Creek, Sylamore Forest, 18 Jun 1945, *Moore 450523* (US); Washington Co., Devils Den State Park, Winslow, 31 May 1936, *Nielsen 3806* (US). Connecticut: Fairfield Co., Bridgeport, 30 Aug 1895, *Eames s.n.* (GH); Hartford Co., Southington, 20 Jul 1898, *Bissell 738* (GH); New Haven Co., Oxford, 11 Aug 1903, *Harger 4490* (GH); New London Co., Franklin, 5 Sept 1904, *Woodward s.n.* (GH); Windham Co., Pomfret, 4 Sep 1916, *Weatherby 4027* (GH*). District of Colum-

bia: E of Rock Creek, Rock Creek Park, S of Boulder Bridge, 22 Sep 1993, *Kanal 475* (US); Woodley Pte., 18 Jul 1899, *Steele s.n.* (US); Cabin John Run, 20 Jul 1930, Morton 1993 (US*). Delaware: New Castle Co., Brandywine Creek, below Bancroft's dam, Wilmington, 16 Aug 1941, *Tatnall 4930* (GH*); Wilmington, 24 Jul 1893, *Common 127* (US*). Georgia: Clarke Co., near Bobbin Mill Creek, alt. 610 ft., 27 Jun 1900, *Harper s.n.* (US); Dade Co., SE of Trenton, 1.3 mi. SE of U.S. route 11 on Georgia route 143, 22 Jun 1973, *Boufford 10151* (GH*), Cloudland Canyon, E of Trenton, 10 Aug 1948, *Cronquist 5624* (US); Gilmer Co., 17 Jul 1973; *Kral 50660* (MO); Stephens Co., W side of Toccoa Falls, 11 Aug 1949, *Duncan 10055* (US); Walker Co., Lookout Mt., 18 Aug 1898, *Ruth 29* (US*); Whitfield Co., 18 July 1900, *Harper 68* (GH*). Illinois: Jackson Co., Makanda, 16 Jun 1903, *Gleason s.n.* (GH*); Jo Daviess Co., Apple River Canyon State Park, S of Apple River, 6 Jul 1941, *Steyermark 40767* (GH); Johnson Co.: Lake of Egypt Recreational Area ca. 3 mi. S of Cereal Springs, 8 Jul 1985, *Mibb 490* (US*); La Salle Co., near Starved Rock, 13 Jul 1901, *Chase 1599* (US); Peoria Co., Peoria, Jul 1904, *McDonald s.n.* (GH*), Peoria Heights, 23 Jun 1959, *Chase 15796* (US); Schuyler Co., along Sugar Creek, 18 Jul 1941, *Evers et al. 575* (GH); Union Co., Southern Illinois University Pine Hills Field Station, 1 Sep 1967, *Poellut 3050b* (MO); Vermilion Co., Middle Fork of the Vermilion River between Oakwood & Collison, 23 Jun 1940, *Jones 11595* (GH, MO); Wabash Co., near Hanging Rock, 4 Sep 1904, *Schneck s.n.* (US); Walworth Co., Laudendale, 15 Jul 1905, *Bebb 2895* (US). Indiana: Crawford Co., "Hemlock Cliffs", ca. 1 mi. S of Miflon, 27 Aug 1970, *Terrell & Meyer 4302* (US), along Little Blue River ca. 1.5 mi. SE of Grantsburg, 9 Jun 1919, *Deam 25593* (US); Daviess Co., terrace of White River, ca. 6 mi. SW of Washington, 2 Jul 1918, *Deam 25593* (US); Hendricks Co., ca. 5 mi. SW of Avon, 13 Jun 1942, *Friesner 16858* (US*); Jennings Co., left branch of the Muscatatuck River, 10 Jul 1911, *Deam 9155* (US); Knox Co., ca. 5 mi. NE of Mt. Carmel, 26 Jul 1925, *Deam 41739* (US); Montgomery Co., N side of Sugar Creek ca. 2 mi. S of Alamo, 17 Sep 1920, *Deam 32824* (US); Posey Co., ca. 4 mi. NW of Mount Vernon, 16 Aug 1919, *Deam 29136* (US); Putnam Co., bank of Raccoon Creek S of Russellville, 28 Aug 1910, *Deam 7423* (US); Steuben Co., 3 mi. W of Angola, 29 Aug 1920, *Deam 32513* (US); Sullivan Co., 1 mi. S of Grayville, 4 Jul 1918, *Deam 25733* (US*); Tippecanoe Co., Lafayette, 20 Jul 1898, *Stuart s.n.* (US); Vanderburgh Co., ca. 7 mi. SW of Evansville, 14 Aug 1919, *Deam 29030* (US); Vigo Co., ca. 2 mi. NE of Riley, 31 Jul 1925, *Deam 41885* (US); Warren Co., Wabash River ca. 2 mi. below Williamsport, 1 Aug 1912, *Deam 11880* (US*); Warlick Co., ca. 2 mi. NE of Yankeetown, 2 Jul 1915, *Deam 16707* (US*). Iowa: 7 Jul 1918, *Powell s.n.* (US*); Allamakee Co., N-facing slope bordering Bear Creek, 15 Jul 1959, *Hartley 7439* (US*); Black Hawk Co., 27 Jul 1929, *Burk 650* (MO); Boone Co., SW of Luther, 15 Jun 1940, *Hayden 8110* (MO); Clayton Co., Pikes Peak, McGregor, 1 Jul 1934, *Fults 2681* (US); Fayette Co., 10 Jul 1894, *Fink 238* (US); Johnson Co., 5 Sep 1909, *Somes 3786* (US); Muscatine Co., Wild Cat Den, 4 Jul 1898, *Ball 11* (ISC, MO, US); Story Co., Ames, 24 Jun 1896, *Ball 43C* (ISC, US**); Webster Co., Woodman Hollow State Park, 15 June 1962, *Freckmann s.n.* (GH); Winnesnick Co., 22 Aug 1903, *Shimek s.n.* (MO). Kentucky: Carter Co., E of Tygarts River, near Cascade Caverns, 4 Jul 1937, *Smith et al. 3456* (GH); Calloway Co., NE of Murray, 24 Jul 1937, *Smith 4208 & Hodgdon* (US*); Clark Co., Pine Ridge road, 5 Aug 1955, *Beckett 868* (US*); Edmonson Co., Mammoth Cave, 1 Jul 1938, *Braun 1987* (US*); Harlan Co., Pine Mountain, Aug 1893, *Kearney s.n.* (MO, US); Muhlenberg Co., Central City, 22 Jun 1932, *Swaller 2285* (GH*); near Harlan Court House, Aug 1893, *Kearney 36* (US*, GH); Letcher Co., Meeting House Branch, Black Mt., 21 Jul 1937, *Braun 1605* (US); Rowan Co., Near Sand Branch, 6 Aug 1974, *Meijer et al. 1130* (MO); Whitley Co., Cumberland Falls, 6 Sep 1939, *Braun 2595* (US*). Louisiana: Caldwell Par., 4 Oct 1988, *Thomas 107627* (MO); East Feliciana Par., Carr's Creek, S of Jackson, 8 Jun 1939, *Brown 7757* (US*); Natchitoches Par., W of Mt. Olive Church, about 2 mi. ENE of Hagedwood, 14 Jun 1967, *Thieret 26833* (US). Maryland: Montgomery Par., Glen

- Echo, 27 Jul 1905, *Chase s.n.* (MO, US***), Bear Island, between the Chesapeake and Ohio Canal and the Potomac River, 23 Jul 1965, Terrell 3893 (US); Prince George's Par, near Collington, Jul 1913, *Maxon* 5986 (US, GH); Washington Par, along Potomac River, W of Snyder's Landing Road, NW of Sharpsburg, elev. 400', 13 Jun 1981, *Hill* 10292 (GH). Massachusetts: Berkshire Co., 3 Aug 1917, *Hunnewell* 5855 (GH*); Bristol Co., W of Segreganset River, Taunton, 19 Jul 1981, *Sorrie* 1094 (GH); Hampshire Co., South Hadley, W of State Rte. 116 opposite Notch Quarry, elev. 410 ft., 13 Sep 1993, *Zebryk* 0794 (GH). Michigan: Kalamazoo Co., Vicksburg, 17 Jul 1940, *Rapp* 4482 (US). Midland Co., bank of Chippewa River, 4 Aug 1934, *Dreisbach* 8287 (GH); Washtenaw Co., 4 mi. S of Ann Arbor, 9 Oct 1924, *Erlanson* 858 (US). Minnesota: Fillmore Co., 2 mi. up the Root River from Peterson, 24 Aug 1943, *Moore* 15998 (GH); Washington Co., N of Copas, Lewis Tree Farm, 12 Sep 1953, *Moore* 21790 & *Rosendahl* (US). Mississippi: Carroll Co., 27 Jun 1960, *McDaniel* 4809 (MO); Tallahatchie Co., W of Mississippi Delta region, Camp Tallaha, 5 mi. S of Charleston, 14 Jul 1956, *Ray* 6930 (GH); Tishomingo Co., along Whetstone Branch, 10 mi. N of Iuka, 7 Aug 1956, *Ray* 7420 (GH). Missouri: Barry Co., 8 mi. S, 1.5 mi. E Cassville, Mark Twain National Forest, 1.75 mi. S jct. Highways 112 and F, from point 0.2 mi down old logging road off E side of Hwy. 112, 14 Jul 1998, *Morse* 2684 (GH); Boone Co., Rock Bridge State Park, 25 Jun 1993, *McKenzie & Campbell* 1236 (MO); Butler Co., 7 Jul 1936, *Steyermark* 11378 (MO); Callaway Co., 7 Jul 1937, *Steyermark* 26204 (MO); Carter Co., Current River, 10 Sep 1897, *Trelease s.n.* (MO); Christian Co., SE of Chadwick, 6 Jul 1937, *Steyermark* 23035 (MO); Clay Co., 12 Jun 1895, *Mackenzie* 763 (MO); Cole Co., 18 Aug 1937, *Steyermark* 24923 (MO); Crawford Co., along Meramec River, 5 mi. W of Steelville, 16 June 1941, *Steyermark s.n.* (GH); Dallas Co., 18 Jul 1934, *Steyermark* 13673 (MO); Franklin Co., Shaw Arboretum of the Missouri Botanical Garden, 18 Jun 1985, *Dawidse & Ellis* 30828 (MO); Gentry Co., 30 Aug 1934, *Steyermark* 15026 (MO); Greene Co., vicinity of Gates, 26 Aug 1912, *Standley* 9391 (US); Hickory Co., E of Jordan, 10 Jul 1934, *Steyermark* 13323 (MO); Howell Co., 9 Jul 1990, *Summers* 3451 (MO); Iron Co., Stony Battery Conservation Area, 2 Jul 1993, *Brant* 2453 (MO); Howard Co., 14 Sep 1937, *Steyermark* 26322 (MO); Jackson Co., Sibley, 10 Sep 1891, *Bush* 1883; Jasper Co., Turkey Creek near Joplin, 12 Jul 1927, *Palmer* 32470 (GH*); Jefferson Co., Wicks, 7 Jul 1898, *Kellogg s.n.* (MO); Laclede Co., SW of Nebo, 23 Aug 1937, *Steyermark* 25153 (MO); Lewis Co., 2 Sep 1937, *Steyermark* 25630 (MO); Macon Co., along Mussel Fork, 4.5–5 mi. SE of New Boston, 14 Sep 1954, *Steyermark* 77266 (US); Madison Co., Jackson Hollow/Marsh Creek, 10 Jul 1996, *Erickson* 65 (MO); Maries Co., NW of Vichy, 16 Sep 1934, *Steyermark* 15291 (MO); McDonald Co., 24 Jul 1893, *Bush s.n.* (MO); Mercer Co., 4 Jul 1933, *Palmer & Steyermark* 41283 (MO); Oregon Co., Greer Spring, 22 Jul 1932, *Steyermark* 7082 (MO); Pery Co., 30 Jul 1934, *Steyermark* 14045 (MO); Polk Co., 17 Jul 1934, *Steyermark* 13636 (MO); Pulaski Co., S of Wildcat Shoals Bridge, 19 Jul 1989, *Ovrebø et al.* W0512 (GH*); Scott Co., SE of Ilmo, 7 Nov 1936, *Steyermark* 20723 (MO); Shannon Co., N of Monteer, 17 Jul 1932, *Steyermark* 7086 (MO); St. Charles Co., 14 Jul 1973, *Dawidse* 3567 (MO); St. Genevieve Co., 27 Jul 1989, *Mohlenbrock* 9095 (MO); St. Louis Co., Allenton, 10 Jul 1898, *Letterman s.n.* (US); Warren Co., Reifsnider Conservtion Area, 8 Jul 1994, *Anderson s.n.* (MO); Texas Co., vicinity of Buck Hollow, 27 Jun 1969, *Pyrhã et al.* 119 (MO); Washington Co., Near Bliss, 31 Jul 1932, *Steyermark* 7023 (MO). Nebraska: Sarpy Co., Near Gretna Fish Hatchery, 29 Jun 1975, *Churchill* 6101 (MO). New Hampshire: Cheshire Co., Surry, 20 Jul 1939, *Knowlton s.n.* (GH). New Jersey: Sussex Co., 10 Aug 1895, *Stockholm n.c.* (US*). New York: Plattsdale, 5 Jul 1921, *Ferguson* 405 (US*); Onondaga Co., Eastwood, 26–28 Jun 1916, *Chase* 7456 (US*); Tompkins Co., N of Beech woods, Six Mile Creek, Ithaca, 5 Jul 1916, *Metcalf* 5629 (GH*); N side of Taughanock Ravine, Ulysses, 1 Aug 1914, *Eames* 1620 (US, GH*); Cascadilla Ravine and vicinity, Ithaca, 10 Jul 1916, *Metcalf* 5630 (GH*); Ithaca, Jul 1884, *Dudley s.n.* (US*); Washington Co., NW of Vaughns, N of Hudson Falls, 19 Jul 1913, *Burnham s.n.* (GH); Westchester Co., Mianus River Gorge Wildlife Refuge and Botanical Reserve, Pound Ridge, 14 Aug 1960, *Soderstrom* 950 (US). North Carolina: 25 Jun 1949, *Brown* 611 & *Clebsch* (US*); Avery Co., Grandmother Mt., 17 Jul 1946, *Hunnewell* 18340 (GH); Buncombe Co., summit of Little Pisgah Mountain, alt. 5300 ft., 28 Jul 1898, *n.c.* 132b (US, GH, MO); Clay Co., between Buck Creek and Perry Gap, 2 Aug 1951, *Godfrey et al.* 51727 (US); Graham Co., 21 Jun 1974, *Boufford* 14501 (MO); Madison Co., French Broad River W of Hot Springs, 23 Jul 1966, *King* 45025 (US*); Mitchell Co., Magnetic City, 8 Jul 1895, *Wetherby* 40 (US); Rutherford Co., Hickory Nutt Falls, Chimney Rock, 5 Jun 1936, *Correll* 7786 & *Blomquist* (US); Swain Co., 15 Jul 1891, *Beardslee s.n.* & *Kofoid* (US*, MO); Transylvania Co., Pink Beds, alt. 3300 ft., 28 Jul 1935, *Correll* 3408 & *Blomquist* (GH); Wake Co., Raleigh, 11 Jul 1938, *Godfrey* 4906 (GH*). Ohio: Adams Co., near Mineral Springs, 30 Jun 1927, *Braun s.n.* (US); Coshocton Co., Mill Creek watershed, North Appalachian Experimental Watershed, near Coshocton, 2 Aug 1942, *Moldenke* 13509 (US); Franklin Co., Columbus, 19 Aug 1907, *Kellerman* 6826 (US); Highland Co., Fors Hill, 28 Jun 1956, *Braun s.n.* (US*); Lake Co., Painesville, Jul 1886, *Werner s.n.* (US*). Oklahoma: Leflore Co., Rich Mt. near Page, 8 Sep 1913, *Stevens* 2675 (GH, MO); McCurtain Co., N of road to Hochatown, 5 Jun 1930, *Little Jr.* 1579 & *Olmsted* (US). Pennsylvania: Berks Co., 1.4 mi NNW of Seifert, 28 Jun 1942, *Berkheimer* 3257 (GH*); Chester Co., Jul 1858–1864, *Sharples s.n.* (GH); Clarion Co., Easton, 13 Jul 1892, *Porter s.n.* (US); Delaware Co., above Levisville, 13 Jul 1899, *MacElwee* 856 (GH*, MO); Tioga Co., Harrison State Forest Park, 9 mi. SW of Wellsboro, 24 Jun 1939, *Fogg Jr.* 16162 (GH*). Rhode Island: Providence Co., Burrillville, 3 Jul 1903, *Knowlton s.n.* (GH). South Carolina: Cherokee Co., 3.3 mi. SW of Blacksburg on US. 29A, 5 Jun 1957, *Ahles* 26998 & *Haesloop* (US*); McCormick Co., along Savannah River 2.5 mi. NW of Clark Hill Dam, 29 Jun 1949, *Duncan* 9813 (US, GH*); Orangeburg Co., Santee State Park, 14 Jun 1988, *Hill* 19583 (MO). Tennessee: Anderson Co., across river from Savage Gardens, Coal Creek, alt. 1500 ft., 12 Jul 1931, *Jennison* 31247 (US); Cheatham Co., Pegram, 25 Jul 1959, *Svenson* 10355 (US*); Cocke Co., 26 Aug 1897, *Kearney* 950 (MO); Coffee Co., 4 mi. SE of Manchester, 3 Aug 1947, *Sharp et al.* 5271 (US); Grundy Co., Tracy City, head of the Fiery Gizzard Cove, 4 Jul 1947, *Shanks et al.* 5326 (US); Henderson Co., Cub Lake, Natchez Trade State Park, 8 Jul 1948, *Sharp et al.* 9322 (US); Marion Co., along Little Sequatchie River near its mouth, 16 Jun 1948, *Fairchild et al.* 48–39 (US); McNairy Co., N of Leapwood, 10 Jul 1948, *Sharp et al.* 9540 (US); Putnam Co., by I-40 just E of Monterey, 2 Aug 1973, *Kral* 51006 (GH, MO); Obion Co., S of Samburg, 17 Jul 1941, *Eyles* 111 & *Eyles* (US, GH); Tipton Co., Craving Spring, near Richardsons Landing, 19 Aug 1947, *Sharp et al.* 6489 (US); Van Buron Co., gorge below Falls Creek Falls, Falls Creek Falls State Park, 29 Jul 1947, *Shanks et al.* 2977 (US); White Co., below Great Falls Dam, near Webb's Camp on Caney Fork, 31 Jul 1947, *Shanks et al.* 5077 (US). Vermont: Addison Co., Leicester, 21 Jul 1938, *Knowlton s.n.* (GH). Virginia: Arlington Co., Potomac River at Chain Bridge, 27 Jul 1935, *Erlanson* 253 (US*); Fauquier Co., Roland, SW base of Bull Run Mts., 2 mi NW of Thoroughfare Gap, 1–2 Sep 1973, *Fosberg* 55115 (US); Greensville Co., along brook entering Nottoway River below Double Bridge, N of Orion, 13 Jun 1940, *Fernald* 11951 & *Long* (GH); James City Co., by James River, Grove Landing, SE of Grove, 29 and 30 Jul 1941, *Fernald* 13233 & *Long* (GH); Lee Co., Limestone glades, The Cedars, 10 Jul 1942, *Carr* 848 (GH); Montgomery Co., Difficult River, Great Falls, 27 Jul 1919, *Leonard* 520 (US*); Page Co., entrance to Matthew's Arm Camp Ground, Shenandoah National Park, alt. 840 m, 18 Aug 1968, *Fosberg* 50466 (US); Scott Co., Natural Tunnel, 5 Aug 1891, *Seymour s.n.* (US*, GH*, MO); Shenandoah Co., North Mountain, 1 Jul 1933, *Hunnewell* 12733 (GH). Smyth Co., mouth of Hungry's Mother Creek, alt. 2075 ft., 4 Jul 1892, *Small s.n.* (US, GH, MO); Spottsylvania Co., along the Rapidan River, 7 Sep 1935, *Erlanson* 4977 (US); Stafford Co., Little Falls, 4 Jul 1896, *Steele s.n.* (US); Surry Co., along James River, Claremont

Wharf, 13 Jun 1938, *Fernald 8052 & Long* (GH*); Washington Co., E side of Big Tumbling Creek, SE side of Clinch Mountain, below boundary of Clinch Mountain State Wildlife Management Area, 4 mi. W of Allison Gap, 7 Aug 1994, *Strong 1204 & Kellogg* (US). West Virginia: Jun 1897, *Millsbaugh s.n.* (US*); Craig Co., Peters Mountain, alt. 760 m., 9 Sept 1903, *Steele 265 & Steele* (GH, US); Greenbrier Co., Allegheny Mountains, White Sulphur Springs, 4 Jul 1920, *Hunnewell 6748* (GH). Mason Co., Glenwood, 17 Aug 1922, *Randolph 1306 & Randolph* (GH). Wisconsin: Dane Co., Madison, 23 Jun 1922, *Showalter s.n.* (GH); Ozaukee Co., Kohler, 6 Aug 1937, *Goessl s.n.* (US); Lafayette Co., 6 mi. E of Gratiot, 22 Jun 1941, *Wadmond et al. s.n.* (US*); Monongalia Co., Morgantown, 1892, *Millsbaugh s.n.* (US); Munroe Co., near Greenville, 5 Jul 1933, *Griscom 18720* (GH*); Rusk Co., 1 mi. E of Ladysmith, 24 Aug 1940, *Shimmers 2758 & Catenhusen* (US); Sauk Co., in the Baraboo Hills near Denzer, 14 Aug 1958, *Hartley 5373* (GH).

CANADA. Ontario: Welland Co., Niagara Falls, 8 Jul 1901, *Fisher s.n.* (US). New Brunswick: Kent Co., Bass River, 30 Jul 1872, *Fowler s.n.* (US).

3. *BRACHYELYTRUM JAPONICUM* (Hack.) Matsum. ex Honda, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 3(1): 210. 1930. Basionym: *Brachyelytrum erectum* var. *japonicum* Hack. Fig. 3c, 6.

Brachyelytrum erectum var. *japonicum* Hack., Bull. Herb. Boissier 7(9): 647. 1899. Type Specimen: 1 of 2. Japan: Koyasan, Prov. Kii [given by Hackel as: Honshu I., Mie—Wakayama Prefect, no date], *J. Matsumura 2* [LT (here designated): Japan, Koyasan, Prov. Kii, W-19818 (electronic image!, courtesy of B. Wallnöfer); IT: US-A8655571* (fragm. ex W-19818)]. 2 of 2. Japan: Sendai, *Faurie 1228* [ST: W-19816].

NOTE: Hackel cited two collections, and there are only two specimens in his herbarium (W) today that can be considered original material (*vide* B. Wallnöfer). Although Hackel indicated no collection number for the *Matsumura* collection, *Matsumura 2* is clearly original material with Hackel's sketchy diagnosis on it. Hackel indicated it was from Mei, Wakiyama Prefect, but the specimen label indicates Koyasan, Prov. Kii. There is a Koyasan, and a Kii-hanto in Wakayama Prefecture, and there is a Kii-nagshima in the Mie Prefecture (*vide* Getty Thesaurus of Geographic Names). Since Mei is not in the Wakayama Prefecture, we suggest that Hackel confused the two Kii's. Of the two cited collections the sheet from *Matsumura* has more material, and the sheet from *Faurie* is immature (*vide* A.S. Hitchcock).

Brachyelytrum erectum subsp. *japonicum* (Hack.) T. Koyama and Kawano, Can. J. Bot. 42: 866, f. 5. 1964. Basionym: *Brachyelytrum erectum* var. *japonicum* Hack.

Culms (37.5–) 39.8–67.2 (–76) cm tall, 0.5–0.9 mm wide at mid-culm; internodes (4.2–) 6.5–11.1 (–11.7) cm long, mostly glabrous; nodes glabrous to pilose. Sheaths (3.7–) 3.8–5 (–5.4) cm long, glabrous to hispid. Ligules 2.0–3.2 mm long, slightly scabrous. Blades (8.1)

8.4–13 (–14.5) cm long, 0.5–0.7 (–0.8) cm wide; abaxially glabrous to sparingly pilose on veins; adaxially glabrous to slightly hispid; margins \pm hyaline, scabrous with 2–19 (–30) prickle hairs per 2 mm of margin and ciliate with 0–10 (–13) macrohairs per 2 mm of margin. Panicles (8.3–) 9.6–15.2 (–18.0) cm long, 0.4–0.8 cm wide with (0–) 1–4 (–5) branches. Spikelets (20.0–) 20.8–28.0 (–30.0) mm long including awns, (9–) 11–15 (–19) per panicle; rachilla (6.89–) 7.2–8.4 (–8.8) mm long. Lower glume (0.2–) 0.4–1.6 (–2.0) mm long; upper glume (0.8–) 1.6–3.6 (–4.8) mm long. Lemmas (0.7–) 0.8–1.0 (–1.2) mm wide; callus short hispid; veins equally prominent, white or green, hispid with hairs 0.1–0.2 mm long, interveinal surface glabrous to scaberulous; awn (9.5–) 11.4–17.4 (–19.4) mm long. Paleas (7.6–) 8.6–10.6 (–11.4) mm long. Anthers 3.3–4.5 mm long. Caryopses 4.5–7 mm long.

Representative Specimens Examined. CHINA. Kuling, Ki., 11 Jul 1935, *DeVol 694* (US*). Anhui: Huang Shan, 7 Jul 1925, *Ching 8558* (US*).

JAPAN. Mt. Koya, Itsu-gun, Wakayama Pref., 1920, *Makino s.n.* (HAST); Awa: Shikoku, Kamibun-kamiyamamura in Nanishigun, 9 Aug 1940, *Inobe s.n.* (US*). Hitachi: Mt. Tsukuba, 29 Jul 1923, *n.c.* (US*). Hondo: Ikaho in Kotsuke, 5 Sept 1950, *Ohwi 71* (US*). Kii: Koyasan, *Matsumura 343* (US); Mitake-Syosenkyo, Yamanasi-ken, 30 Jul 1954, *Tateoka s.n.* (ISC, US*); Settsu: Honshu, Dojomura in Arimagun, 17 Jul 1955, *Togasi 1196* (US*, GH*); Settsu, 23 Jul 1903, *Arimoto s.n.* (GH*).

KOREA. Quelpart, 12 Aug 1908, *Taquet 1928* (US*, GH*).

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