
Taxonomic Innovations in North American *Eleocharis* (Cyperaceae)

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ABSTRACT. Taxonomic innovations for the upcoming volume 23 of the *Flora of North America* (FNA) are here published. *Eleocharis quinqueflora* (F. X. Hartman) O. Schwarz, *E. suksdorfiana* Beauverd, and *E. bernardina* (Munz & I. M. Johnston) Munz & I. M. Johnston are redefined. New taxa described are: *E. occulta* S. G. Smith, segregated from *E. acutisquamata* Buckley; *E. bifida* S. G. Smith, segregated from *E. compressa* Sullivant; *E. torticulmis* S. G. Smith, segregated from *E. suksdorfiana*; and *E. acicularis* (L.) Roemer & Schultes var. *porcata* S. G. Smith, confused with *E. wolfii* (Gray) Gray. Other innovations are: *E. elliptica* Kunth var. *atrata* (Svenson) S. G. Smith, comb. nov.; *E. compressa* var. *acutisquamata* (Buckley) S. G. Smith, stat. nov.; *E. palustris* (L.) Roemer & Schultes var. *vigens* L. H. Bailey, lectotypified.

Key words: Cyperaceae, *Eleocharis*, North America.

Taxonomy in *Eleocharis* is confused because of morphological convergence in habit, vegetative reproduction (tubers, bulbs, stolons, viviparous spikelets), and most structures including culms, leaf sheaths, spikelets and their scales, perianth bristles, style branches, tubercles, and achenes (Gonzalez-Elizondo & Peterson, 1997; Gonzalez-Elizondo et al., 1997; Roalson & Friar, 2000).

This paper contains taxonomic innovations resulting from my work on the treatment of *Eleocharis* for the upcoming volume 23 of the *Flora of North America* (FNA) (Flora of North America Editorial Committee, in press).

Eleocharis is a worldwide genus comprising about 200 species (Gonzalez-Elizondo & Peterson, 1997). The latest comprehensive taxonomic treatment for North America was done by Svenson (1957), who recognized 61 species. About 65 species will be recognized in the FNA treatment. Gonzalez-Elizondo and Peterson (1997) provided a supraspecific classification utilizing four levels of taxonomic categories, which will be followed.

Classification of *Eleocharis* is unusually difficult for two main reasons: (1) The simple structure (unbranched aerial stems; only two leaves, which are basal, sheathing, and without blades or with only

rudimentary blades; and a single terminal spikelet without involucre bracts) provides relatively few macroscopic characters. (2) *Eleocharis* includes several extremely difficult species complexes needing taxonomic revision. Many of the species in these complexes have never been precisely defined. Problems of species delimitation are probably due in part to interspecific hybridization, which has been studied mainly in the *E. palustris* complex in Europe (Strandhede, 1965, 1966). Unstable chromosome structure, polyploidy, and aneuploidy associated with diffuse-centromere chromosomes and aberrant meiosis and pollen development (Harms, 1968, 1972; Strandhede, 1965, 1967) doubtless also contribute to taxonomic complexity. This paper resolves some of the taxonomic problems in the *E. palustris* complex, the *E. tenuis-compressa* complex, the *E. quinqueflora* complex (*E.* subg. *Zinserlingia* T. V. Egerova), and the *E. acicularis* complex (*E.* subg. *Scirpidium* (Nees) Kukkonen) in North America.

A. THE *ELEOCHARIS PALUSTRIS* COMPLEX

The *E. palustris* complex comprises subgenus *Eleocharis* sect. *Eleocharis* ser. *Eleocharis* subser. *Eleocharis* (= *E.* ser. *Eleocharis* subser. *Palustres* Svenson). It is circumboreal and comprised of perhaps 10 to 15 species. All of the North American and Eurasian species are difficult to delimit. Strandhede (1965, 1966) studied extensively the 4 species of this complex in northern Europe. It is still poorly understood in North America, for which Svenson (1957) recognized 6 species. I recognize 7 species, which include all 4 European species. For Europe, Strandhede (1966) showed that interspecific hybridization and polyploidy are a major cause of taxonomic difficulties among the species recognized there, and by extrapolation it seems likely that hybridization and polyploidy are also important in North America.

The most widespread and variable species in this complex is the circumboreal *E. palustris* (L.) Roemer & Schultes, within which I am including the North American *E. smallii* Britton as a synonym. For North America, Strandhede (1967) distin-

guished two groups with the morphology of *E. smallii*: (1) $2n = 16$ -chromosome plants with achenes 1.2–1.5 mm and culm stomata 39–48 μm long, and (2) $2n = 36$ -chromosome plants with achenes 1.6–1.7 mm and stomata 55–60 μm long. Harms (1968) also reported both $2n = 16$ and $2n = 36$ for *E. smallii* in North America. In Europe $2n = 16$ plants of *E. palustris* are placed in subspecies *palustris* and $2n = 38$ or 39 plants are placed in subspecies *vulgaris*, which differs from the North American plants of *E. smallii* with large achenes in having a morphology intermediate with that of *E. uniglumis* (Link) Schultes. I have measured the achenes of Britton's type of *E. smallii* as ca. 1.3×1.1 mm and the stomata as 39–43 μm long. Therefore, pending a much needed worldwide taxonomic revision of the *E. palustris* complex, it is desirable to use a name based on a North American type for North American plants like the type of *E. smallii* except for larger achenes and longer stomates associated with $2n = 36$ chromosomes. Hooker's earlier varietal names from Saskatchewan and Lake Huron cannot be used because Hooker's descriptions in the protologue (in *Fl. bor.-Amer.* 2: 228. 1839) conflict with the morphology of the robust polyploid plants. His descriptions read in their entirety: *E. palustris* Br . . . " β minor: spica ovata" and " γ degenerata: bi-triuncialis, spica minima 3–5 flora." The following is the only available and acceptable name for these plants:

- 1. *Eleocharis palustris* (L.) Roemer & Schultes**
var. **vigens** L. H. Bailey, *J. New York Microscop. Soc.* 5: 104. 1889. TYPE: U.S.A. Vermont: Franklin Co., shore of Lake Champlain, Highgate Springs, Aug. 1813, *H. G. Jessup s.n.* (lectotype, selected here, GH).

Bailey cited four syntypes in the protologue. Of these only one specimen at GH has been located after searches at GH and BH, and this is selected here as the lectotype.

The lectotype consists of three culms with spikelets in good condition. The few mature achenes are 1.75×1.35 – 1.5 mm. The culm stomates are ca. 60 μm long. The culms are 2.5–3 mm thick when not pressed flat. The following specimens were collected at or near the syntype localities and are very similar to the lectotype: U.S.A. New York: Erie Co., shallow water N of Buckhorn Island, Niagara River, 27 Aug. 1928, *W. C. Muenscher 17160* (BH); shallow water around Strawberry Island, Niagara River, 21 Aug. 1928, *W. C. Muenscher 17159* (BH). Vermont: Chittenden Co., Shelburne Bay, Lake Champlain, 26 Aug. 1926, *W. C. Muenscher & B. Ma-*

guire 275 (BH) [stomata 59–65 μm]. I have seen very similar specimens from Canada: Manitoba (Churchill), New Brunswick, Newfoundland, Nova Scotia, Ontario, Quebec, Isle of Miquelon; U.S.A.: Maine, Michigan, Nebraska, New York, Wisconsin.

Plants of *E. palustris* var. *vigens* are ca. 50–120 cm tall, and the culms (not pressed flat) are ca. 1.5–4 mm thick, which is very robust compared to most other *E. palustris* plants. They are often emergent in water to ca. 1 m deep.

B. THE *ELEOCHARIS TENUIS-COMPRESSA* COMPLEX

This complex is part of *Eleocharis* subg. *Eleocharis* sect. *Eleocharis* ser. *Eleocharis* subser. *Truncatae* Svenson. It is restricted to North America, where it is widespread except in the Southeast and Southwest. Svenson (1957) recognized the following five species: *E. tenuis* (Willdenow) Schultes, in Roemer & Schultes, *E. elliptica* Kunth, *E. compressa* Sullivant, *E. acutisquamata* Buckley, and *E. nitida* Fernald. I recognize *E. tenuis*, *E. elliptica*, *E. compressa*, *E. nitida*; and *E. bifida* S. G. Smith and *E. occulta* S. G. Smith, both described herein.

Except for *E. nitida*, species delimitation in this complex is difficult because many plants are intermediate between *E. tenuis* and *E. elliptica*, between *E. elliptica* and *E. compressa*, and between *E. compressa* and *E. acutisquamata*. Also, a few plants are intermediate between *E. compressa* and *E. tenuis* var. *verrucosa* (Svenson) Svenson. Some authors (Boivin, 1979; Gleason, 1968; Gleason & Cronquist, 1991; Taylor, 1983) have dealt with these intermediates by combining two or more species. Combining these species, however, effectively obscures differences in morphology, ecology, and distribution that are useful in ecology and other fields. Therefore, it is preferable to more precisely define the species that have long been recognized, and to recognize them whenever most specimens can be identified with confidence.

The many plants intermediate between *E. compressa* and *E. elliptica* led Drapalik and Mohlenbrock (1960a, 1960b) and Rolfsmeier (1995) to combine them, while other authors (Voss, 1972; Swink & Wilhelm, 1994) have maintained them as distinct species. I have defined *E. elliptica* broadly to include some plants often included under *E. compressa* (see Voss, 1972). Most specimens can be identified with confidence to *E. elliptica*, *E. compressa*, *E. occulta*, or *E. bifida*. My field observations in southeastern Wisconsin and herbarium studies suggest that the intermediate plants are hybrids and that there is considerable reciprocal introgression. The new status *E. elliptica* var. *atrata*

(Svenson) S. G. Smith made herein provides a varietal name in which to place the plants of *E. elliptica* that approach *E. compressa*.

As currently defined the only differences between *E. compressa* and *E. acutisquamata* seem to be that *E. compressa* has distinctly compressed culms and is mostly eastern, whereas *E. acutisquamata* has subterete culms and occurs mostly in the Great Plains. Svenson (1966, Appendix herein) stated that *E. acutisquamata* should be included under *E. compressa*.

However, my studies show that there are two groups of specimens that have been included within *E. compressa* and *E. acutisquamata* but clearly deserve species status. These groups differ strikingly from both typical *E. acutisquamata* and *E. compressa* and from each other. In these two groups the proximal scale and all of the floral scales are bifid, and the rhizomes and their scales are obscured by the living and dead culm bases. In contrast, in both typical *E. acutisquamata* and typical *E. compressa* the proximal scale of the spikelet is entire and the floral scales vary from bifid to entire, often in the same spikelet, and the rhizomes and their scales are clearly evident, not obscured by culm bases. One of these groups, which has been included in *E. compressa*, has extremely broad, compressed culms, and is known only from Tennessee and adjacent Georgia, Alabama, and Kentucky; it is herein described as *E. bifida*. The other group, which has been included in *E. acutisquamata*, has very slender, subterete culms and is known only from Texas and Oklahoma; it is herein described as *E. occulta*. The remaining plants comprise an extremely morphologically variable group within which it is impossible to clearly distinguish segregate taxa. A satisfactory treatment of these remaining plants is to combine them under *E. compressa* with two varieties as is accomplished herein.

1. *Eleocharis elliptica* Kunth var. *atrata* (Svenson) S. G. Smith, stat. nov. Basionym: *Eleocharis compressa* var. *atrata* Svenson, *Rhodora* 34: 218. 1932. *Eleocharis elliptica* forma *atrata* (Svenson) Drapalik & Mohlenbrock, *Amer. Midl. Naturalist* 64: 20. 1960. *Eleocharis tenuis* var. *atrata* (Svenson) Boivin, *Provancheria* 25: 63. 1992. TYPE: U.S.A. Pennsylvania: Presque Isle, Erie, 18 June 1910, A. S. Pease 12881 (holotype, GH).

The type is complete, with rhizomes and many mature achenes. It approaches *E. compressa* var. *compressa* in its stout rhizomes with very short internodes, slightly compressed culms (ca. 1.2–2×

wider than thick) with up to 8 prominent ridges, and its floral scale apices cut ca. 0.5–0.7 mm deep. However, it is much more like *E. elliptica* in its achenes and tubercles as well as in the presence of a stout tooth on many distal leaf sheath summits.

My field observations in Wisconsin indicate that typical *E. elliptica* grows in permanently wet habitats such as those found in many groundwater discharge areas in fens, whereas *E. compressa* grows in places such as depressions in prairies and exposed limestone that are often dry in summer. *Eleocharis elliptica* var. *atrata* grows in such habitats as the drier parts of fens that are intermediate between those of typical *E. elliptica* and those of *E. compressa*.

2. *Eleocharis bifida* S. G. Smith, sp. nov. TYPE: U.S.A. Tennessee: Wilson Co., industrial park development just S of Hwy. 40 on E side of Lebanon, disturbed limestone glade, 19 May 1992, S. G. Jones & R. Kral 8684 (holotype, TENN; isotypes, MICH, SAT, USF, VSC). Figures 1, 2.

Species *E. compressae* affinis sed rhizomatibus culmis tectis, (3–)4–5 mm crassis, culmis compressis magnopere 4–10-plo latis quam crassis, stylis omnibus trifidis, fructibus omnibus trigonis teretis fere vel compressis leviter differt.

Densely caespitose; (8–)20–35 cm. *Rhizomes* concealed by living and persistent dead culm bases, short; (3–)4–5 mm thick; hard; internodes too short to measure; scales decaying to coarse fibers, ca. 1 cm, papery, fibrous. *Culms* greatly compressed, cross section narrowly oblong, ca. 4–10× wider than thick, often with 1 or 2 sharp ridges on one side; 0.7–2.3 mm wide; hard; finely striate; internally spongy. *Distal leaf sheaths* persistent, not splitting; proximally red or stramineous, distally green to stramineous; papery; summits inflated, dark brown, callose; apices broadly obtuse to subtruncate; tooth absent. *Spikelets* ovoid, acute; 4–9 × 2.5–4 mm. All *scale* apices bifid. *Proximal scale* without a flower, clasping ca. 2/3–3/4 of culm. *Subproximal scale* with or without a flower. *Floral scales* spreading in fruit; ca. 30 to 60, 6 to 9 per mm of rachilla; medium or pale brown, midrib region often narrowly paler; ovate-lanceolate; carinate in distal part of spikelet; 2.5–3.5 × 1.5 mm. *Perianth bristles* 0(to 5); stramineous to pale brown; ca. half of to equaling achene, densely to sparsely retrorsely spinulose. *Stamens* 3; anthers orange-brown, ca. 0.7–1.5 mm, apices apiculate. *Styles* all trifid. *Tubercles* brown; depressed-pyramidal, often rudimentary; 0.1–0.25 × 0.2–0.3 mm. *Achenes* falling with scales; dark yellow when unripe, yellow- to medium

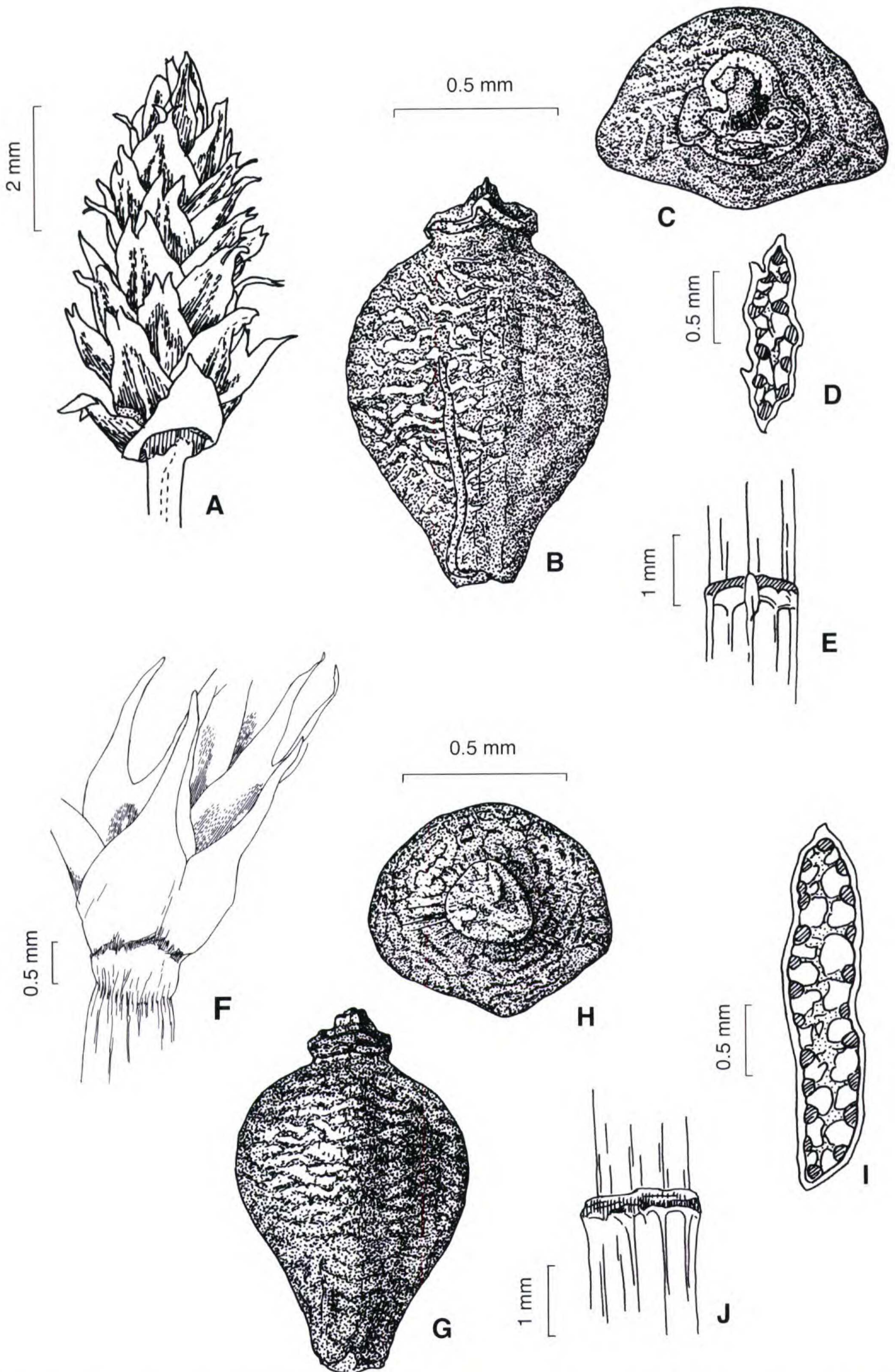


Figure 1. A–E, *Eleocharis compressa* Sullivant var. *compressa*. —A. Spikelet. —B, C. Achenes. —D. Culm cross section. —E. Distal leaf sheath summit. F–J, *Eleocharis bifida* S. G. Smith. —F. Proximal part of spikelet. —G, H.

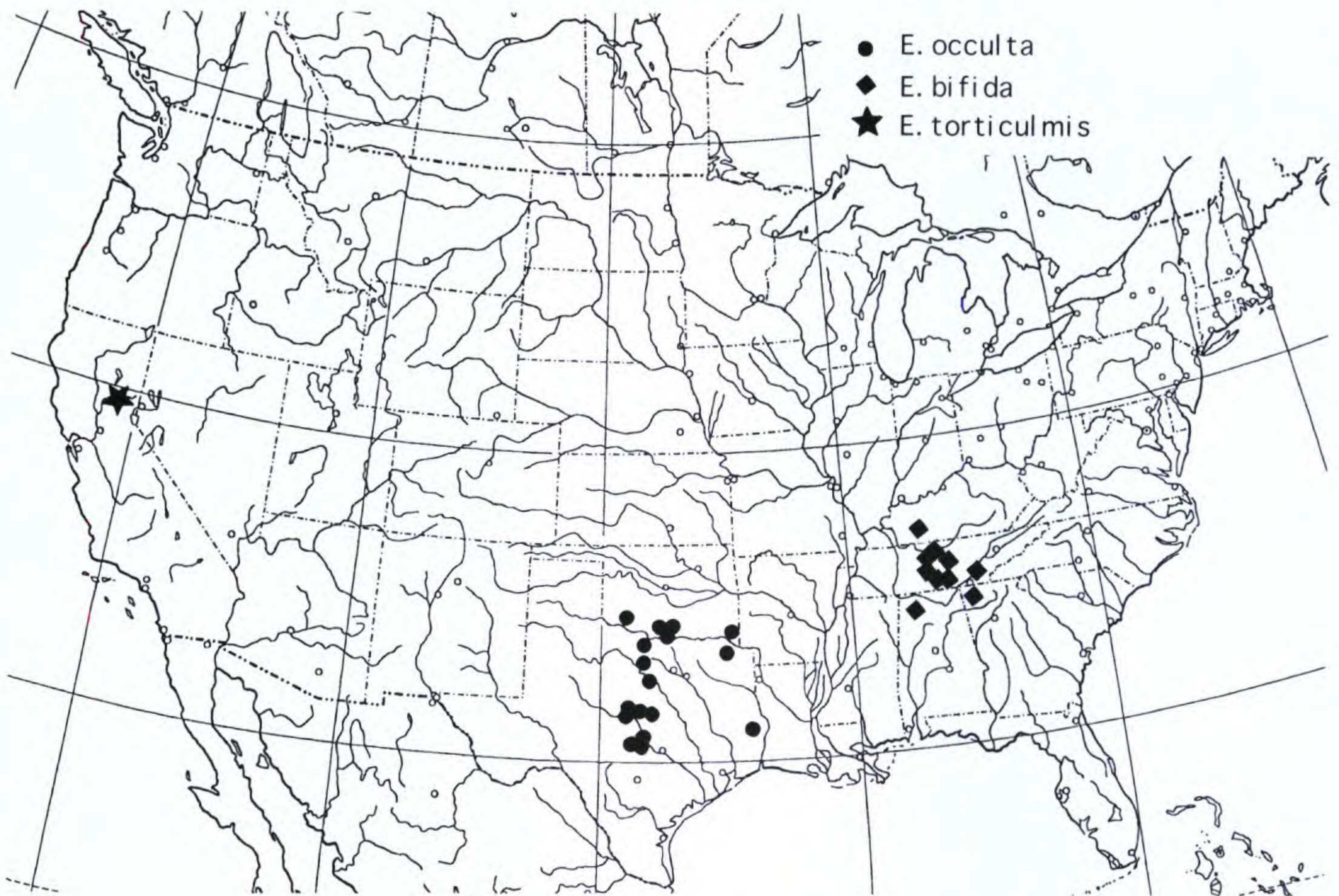


Figure 2. Known distribution of *Eleocharis bifida* S. G. Smith (diamonds), *Eleocharis occulta* S. G. Smith (circular dots), and *E. torticulmis* S. G. Smith (star).

brown when ripe; obovoid to obpyriform, neck usually very short; trigonous, nearly terete to slightly compressed, angles obscure or evident; $0.9\text{--}1.1 \times 0.6\text{--}0.75$ mm; finely rugulose at $10\text{--}30\times$, with 20 or more low, blunt horizontal ridges in a vertical series.

Distribution and ecology. *Eleocharis bifida* is currently known only from Tennessee, Alabama, Georgia, and Kentucky (Fig. 2). Its typical habitat as given on collection labels is seeps and other wet places in forest openings ("barrens" or "glades") on limestone. The label of *Svenson 13059* from Montgomery Co. states: "clumps in wet meadow with *Eleocharis wolfii*, *E. tenuis* var. *verrucosa*, *E. tenuis* var. *pseudoptera*, *Carex shortiana*." The label of the type specimen states: "disturbed limestone glade with calcareous clay soil and limestone, with *Carex*, *Penstemon*, *Dalea*, *Sphenopholis*, *Euphorbia*, *Bromus*, *Melica* and *Juncus*." The label of *Svenson 7148* from Wilson Co. states: "dried-out beds of shallow streams." Other habitats given are prairie,

roadside ditch, and rocky pasture. The only reported elevation I have seen is ca. 200 m. Flowering and fruiting are in May and June.

The epithet *bifida* describes the bifid spikelet scales, including the proximal scale.

Eleocharis bifida has previously been included in *E. compressa*, which differs (as defined below) consistently and qualitatively as follows (refer to Figs. 1 and 3): *Rhizomes* evident, not obscured by culm bases rather than obscured (as in *E. occulta*, Fig. 3). *Proximal scales* of spikelets entire. *Eleocharis compressa* also differs, with some overlap of measurements or character states, as follows: *Rhizomes* 2–3 mm thick, internodes to 2 mm. *Culms* (0.3–)0.5–1.5 mm wide, ca. 1–5 \times wider than thick when dry, usually with prominent sharp ridges. *Floral scales* usually bifid in the proximal half and entire in the distal half of the spikelet, less commonly all bifid, rarely all entire. *Styles* often trifid and bifid in the same spikelet. *Achenes* compressed-trigonous or often some biconvex in the

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Achenes. —I. Culm cross section. —J. Distal leaf sheath summit. A, drawn from *Monson 1886* (ISC); B, drawn from *Correll & Correll 37307* (LL); C, drawn from *Clokey 2375* (WIS); D, drawn from *Mackenzie s.n.*, Sussex Co., N.J. (NY); E, drawn from *Clokey 2375* (NY); F, drawn from *Busing 80-158* (TENN); G, H, and J, drawn from *Kreibel 9850* (NY); I, drawn from *McNeilus 88-518* (WIS).

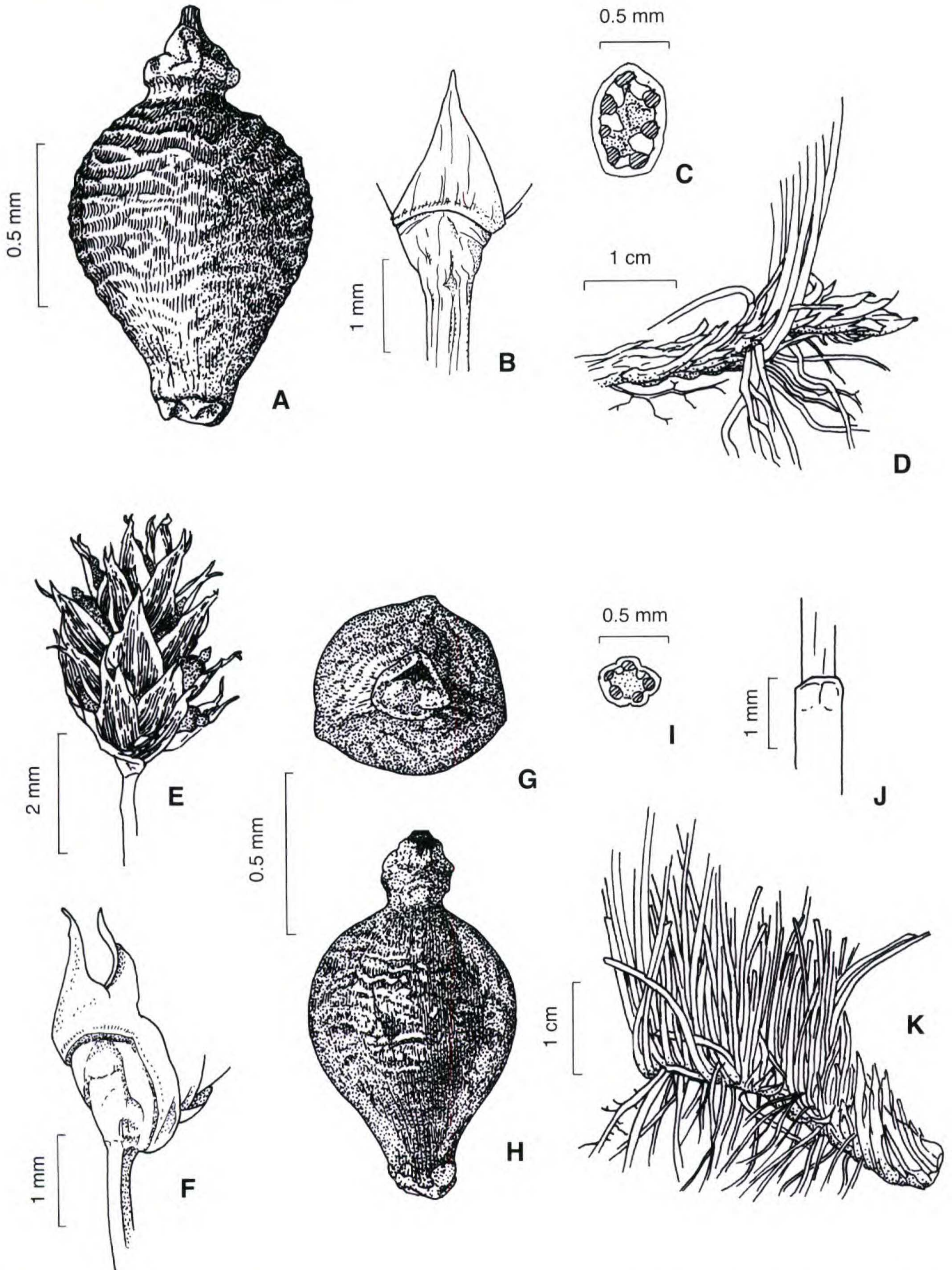


Figure 3. A–D, *Eleocharis compressa* Sullivant var. *acutisquamata* (Buckley) S. G. Smith. —A. Achene. —B. Proximal scale of spikelet. —C. Culm cross section. —D. Rhizome and proximal part of culm tuft. E–K, *Eleocharis occulta* S. G. Smith. —E. Spikelet. —F. Proximal scale of spikelet. —G, H. Achenes. —I. Culm cross section. —J. Distal leaf sheath summit. —K. Portion of rhizome and proximal part of culm tuft (at left). A, drawn from Correll & Correll 37307 (LL); B to D, drawn from Lundell 13663 (LL); E and G to I, drawn from Bridges & Kindscher 13591 (LL); F, drawn from Oefinger 355 (TEX); J and K, drawn from Lundell & Lundell 10298 (LL).

same spikelet, the abaxial angle evident or lacking, usually finely rugulose at 10× (20×).

Eleocharis bifida is morphologically very constant, whereas *E. compressa* is highly variable. A few specimens from similar habitats in Tennessee and adjacent Alabama and Kentucky resemble *E. bifida* except for their entire proximal spikelet scales and/or evident rhizomes. *Eleocharis bifida* is known only from south of the limits of Pleistocene glaciation, whereas *E. compressa* occurs mostly in glaciated regions.

Paratypes. U.S.A. **Alabama:** Franklin Co., seepage area on cedar glade 1 mi. N of Richardson's Crossing, ca. 7 mi. E of Russellville, 1961, *E. E. Terrell & A. S. Barclay* 3503 (FSU). **Georgia:** Catoosa Co., Chickamauga Natl. Battlefield Park, 20 mi. N of Viniard, 1990, *D. F. Brunton & K. L. Mcintosh* 9587 (MICH). **Kentucky:** Logan Co., limestone glade on Lula Davis farm 0.8 mi. on Duncan Chapel Rd. from US 68E, 1977, *R. Athey* 3730 (FSU). **Tennessee:** Coffee Co., prairie 4 mi. SE of Manchester, 1947, *R. E. Shanks et al.* 5184 (TENN); Davidson Co., Mt. Juliet Rd., 4.8 mi. S of I-40, Couchville Barrens, 1988, *V. E. McNeilus* 88-518 (FLAS, NDA, TENN, WIS); along Nashville Rd. near Lavergne, cedar glades, 1938, *H. K. Svenson* 8712 (CAS, GH, MO, NY, TENN, WIS); Davidson Rd. ca. 5 mi. W of Nashville, 1942, *J. M. Shaver* 2587 (BRIT, TENN); Marshall Co., 2.1 mi. ESE of Pottsville on Tenn. Rte. 99, limestone glade, 1969, *R. Kral* 34780 (MO); along Tenn. Rte. 99 ca. 2.0 mi. W of Rte. 31A, 1998, *V. E. McNeilus* 98-212 (TENN); Maury Co., open glade 1.8 mi. W of Bryant Station along Tenn. Rte. 50, SE of Columbia, 1966, *R. Kral* 26697 (KANU); Meigs Co., jct. of Tenn. Rte. 58 & 60, 1992, *V. E. McNeilus* 92-518 (FLAS, LSU, MICH, NDA, TENN, WIS); barren at NW corner of jct. of Tenn. 58 & 60, 1987, *H. R. DeSelm s.n.* (TENN); Montgomery Co., King-Queen Bluff on Cumberland River 3 mi. ESE of Clarksville, 1950, *A. Clebsch* 12915 (TENN); Rutherford Co., Murphreesboro, S side of East Clark Blvd., 1954, *H. K. Svenson* 13059 (TENN, WIS); limestone barren opposite Stones River, Mil. Park, N of Murphreesboro, 1959, *A. J. Sharp* 25892 (TENN); U.S. Hwy. 231 W of Christiana, 1959, *A. J. Sharp* 25915 (TENN); Sharp's Barren opposite entrance to Stone's River Military Park NW of Murphreesboro, 1958, *H. R. DeSelm* 1776 (TENN); roadside ditch along Rd. 10 about 10 mi. N of Murphreesboro, 1941, *C. C. Deam* 61392 (KANU); Wilson Co., Cedars of Lebanon Park, Vine Quadrangle, 3.75 mi. W of U.S. Hwy. 231, 1980, *W. Manek* 12 (TENN); cedar glades 7 mi. N of Murphreesboro, 1942, *R. M. Kriebel* 9850 (NY); E side of Rd. 10, 11 mi. S of Lebanon, 1941, *R. M. Kriebel* 9452 (NY); Lebanon State Forest near Cedars of Lebanon State Park, E of U.S. Rte. 231, 1995, *S. R. Hill* 26246 (ILIS, USF); cedar glade along Cedar Forest Rd., 2.0 mi. W of U.S. Hwy. 231, Vine Quadrangle, 1980, *R. Busing* 80-158 (TENN); Sinking Creek, S side of Lebanon, 1969, *K. E. Blum* 3414 (TENN); N side of county road ca. 2 mi. E of Vesta and 4 mi. SE of Gladeville, 1977, *D. H. Webb et al.* 884 (TENN); Cedars of Lebanon Forest rd. ca. 1.8 mi. W of Rte. 231, 1990, *V. E. McNeilus* 90-235 (NDA, TENN, WIS); limestone barrens near Gladeville, 1960, *F. A. Swink* 3385 (F).

3. *Eleocharis occulta* S. G. Smith, sp. nov.
TYPE: U.S.A. Texas: Montague Co., just W of Forestburg, in water in edge of small pond, in clumps, 28 Apr. 1964, *D. S. & H. B. Correll* 29501 (holotype, LL; isotype, GH). Figures 2, 3.

Species *E. compressae* Sullivant et *E. acutisquamatae* Buckley affinis sed rhizomatibus culmis tectis, culmis teretibus, squamis spicularum omnibus bifidis, stylis omnibus trifidis, fructibus omnibus trigonis, teretis fere, rugulosis obscure differt; ab *E. bifida* culmis teretibus, squamis spicularum 2–2.8 mm longis, circa 1 mm latis, apicibus lanceolatis-attenuatis differt.

Densely caespitose; 27–56 cm. *Rhizomes* concealed by living and persistent dead culm bases, often ascending, short; 3–5 mm thick; hard; cortex persistent; internodes very short; scales decaying to coarse fibers, ca. 5–12 mm long, papery. *Culms* subterete, sometimes slightly compressed, with 4 to 7 blunt ridges when dry; 0.2–0.5(0.7) mm wide; firm to hard; spongy. *Distal leaf sheaths* persistent, not splitting; proximally red, distally green to stramineous; thinly papery to thinly membranous, sometimes hyaline; summits often inflated, often callose; apices broadly obtuse to subtruncate; sheath tooth absent. *Spikelets* ovoid, acute; 3–10 × 2–3 mm. All *scale* apices bifid. *Proximal scale* amplexicaulous. *Floral scales* deciduous, spreading in fruit; ca. 20 to 50, with 7 per mm of rachilla; medium brown, midrib region often narrowly stramineous; apices lanceolate-attenuate; carinate; 2.0–2.8 × ca. 1 mm. *Perianth bristles* 3 or absent, stramineous to pale brown, rudimentary to about half of achene, sparsely obscurely retrorsely spinulose. *Stamens* 3, anthers orange-brown, thecae 0.7–1.3 × 0.25 mm, apex acute. *Styles* trifid. *Tubercles* brown, depressed-pyramidal, often rudimentary; 0.1–0.15 × 0.2 mm. *Achenes* falling with scales, dark yellow ripening to medium or dark brown, obpyriform, neck distinct, rarely absent; obscurely trigonous, nearly terete; 0.7–1.0 × 0.5–0.65 mm; obscurely rugulose at 10–30×, 30 or more low, blunt horizontal ridges in a vertical series.

Distribution and ecology. *Eleocharis occulta* is known only from Oklahoma and Texas (map, Fig. 2) but is expected from adjacent states. It flowers and fruits from March to May, sometimes as late as July. Reported habitats include seasonally wet seepages, depressions, swales, rock crevices, rocky streambeds, stream banks, wet meadows, pond margins, temporary pools, and juniper-oak glades, often on limestone (rarely granite) or evidently calcareous soils, the soils sometimes dry. Elevations reported

are ca. 75–325 m. Flowering and fruiting are in March to May.

The epithet *occulta* describes the hidden nature of the rhizomes, concealed by the culm bases. *Eleocharis occulta* was previously included in *E. acutisquamata*, the remainder of which is herein treated as *E. compressa* var. *acutisquamata*.

Eleocharis compressa consistently and qualitatively differs from *E. occulta* as follows: *Rhizomes* not hidden by culm bases (Fig. 3). *Proximal scale* of spikelets entire (Fig. 3). *Eleocharis compressa* inconsistently differs, with some overlap of character states, as follows: *Rhizome* internodes to ca. 2 mm. *Culms* often greatly compressed, to 1.8 mm wide and 5× wider than thick. *Floral scale apices* usually bifid or deeply cut toward spikelet base and merely bidentate or entire toward spikelet apex, sometimes all entire. *Styles* often trifid and bifid in the same spikelet. *Tubercles* often well developed. *Achenes* usually without a pronounced neck, commonly compressed trigonous or lenticular, angles usually evident, often clearly rugulose at 10–20×, ca. 14–20 rows of ridges in a vertical series.

Eleocharis occulta is morphologically very constant, whereas *E. compressa* is extremely variable. Like *E. bifida*, *E. occulta* occurs only south of the limits of Pleistocene glaciation, where it presumably survived glaciation in more or less its present range. Although *E. occulta* is sympatric with *E. compressa* var. *acutisquamata* throughout its range, no intermediates are known.

Paratypes. U.S.A. **Oklahoma:** Comanche Co., Wichita Mts., N slope of Elk Mountain, 1958, L. M. Rohrbaugh 519 (KANU, OKL, OKLA); Wichita Mts. Natl. Wildlife Refuge, 1/2 mi. N of Grama Flat Lake, 1942, F. B. Mc Murry 1150 (OKL); Wichita Mts. NWR Treasure Lake area, 1979, C. Taylor 27414 (BRIT, TENN); Wichita Mts. NWR, Cado Lake, 1986, L. K. McGrath & W. Wilson 16610 (OKLA); Wichita National Forest, Panther Creek, 1937, C. T. Eskew 1626 (OKL); Hamilton Co., 7 mi. E of Hamilton, 1969, J. W. Stanford 21 (OKLA); Johnston Co., Bee Branch ca. 5 mi. SW of Mill Creek, 1976, J. Taylor 22082 (BRIT); McCurtain Co., limestone ridge 2 mi. E and 2 N of Idabel, 1969, U. T. Waterfall 17434 (OKLA); Garvin 1936, D. Demaree 12034 (OKL); Murray Co., near Crusher Spur, 1913, G. W. Stevens 24 (BRIT, DS, GH, OKL, OKLA); Arbuckle Mts., ca. 3/4 mi. W of Camp Classen, 6 mi. S of Davis, 1948, R. Stratton 6800 (CAS, NY, OKLA); below Arbuckle Dam, 1994, F. L. Johnston et al. 0150 (OKL); Arbuckle Mts., Davis, 1936, D. Demaree 12512 (OKL); Arbuckle Mts., R2E T1S Sec 30, 1.3 mi. SW of I-Hwy. 35 on U.S. Hwy. 77D, 1973, R. J. Tyril 746 (OKL, USF); near stream in Cowpen Canyon, Corbert Porphyry, 194[8?], E. E. Dale 290 (OKL); near Honey Creek, Frank's Conglomerate, 1942, E. E. Dale 87 (OKL); Rock Creek SW of Veteran's Lake, 1996, B. Hoagland & D. Benish 0794 (OKL); Arbuckle Mts., Cow Pen Creek running through Frank's conglomerate, 1941, M. Hopkins 5966 (OKL); Sulphur, Platt National Park, 1936, D. De-

maree 12250 (TEX); Pontotoc Co., Wintersmith Park 1 mi. S of Ada, 1952, D. McCoy 2344 (OKLA). **Texas:** Blanco Co., Federales Falls State Park, 1992, S. Oefinger, Jr. 355 (TEX); Little Blanco River 8 mi. S of Blanco, 1966, J. R. Crutchfield 1206 (NY); Brown Co., 2 mi. W of Brownwood, 1968, J. W. Stanford 2103 (OKLA); Hays Co., San Marcos, 1885, N. T. Kidder s.n. (KANU); Hamilton Co., seepy roadside ditch adjacent to prairie with limestone outcrops, ca. 11–12 mi. S of Hamilton, 1990, E. L. Bridges & K. Kindscher 13591 (TEX); McCulloch Co., 4 mi. SE of Brady, 1963, D. S. Correll, E. C. Ogden & H. K. Svenson 28259 (F, LL, NY, UC); McLennan Co., Hog Creek, 1947, L. D. Smith 473 (TEX); Red River Co., White Rock, 1963, D. S. Correll 27268 (LL, UC); San Augustine Co., 1.1 mi. E of center of San Augustine, 0.2 mi. SW of gravel road to Sunrise, 1988, S. L. Orzell & E. L. Bridges 6871 (TEX); about 1 mi. SW of San Augustine, 1962, D. S. Correll 25004 (LL, NY 2 sheets); road to S of Rte. 21 at E edge of San Augustine, 1964, D. S. & H. B. Correll 29081 (LL); San Saba Co., 14 mi. SW of Richmond Springs, 1977, P. Bursleson 744 (SAT); Tarrant Co., main road 0.8 mi. SE of N gate, Natl. Guard Eagle Mountain Lake Training Area, Avondale Quadrangle, 1993, W. R. Carr 12802 (TEX); Travis Co., Edwards Plateau near Austin, 1921, B. C. Tharp s.n. (UC); 14 mi. W of Austin, 1921, B. C. Tharp 995 (GH, NY), 1921, B. C. Tharp 996 (F, ISC, NY); ravine between Cypress and Sandy Creeks up the Colorado River, Austin, 1921, B. C. Tharp 998 (CAS, TEX); temporary pool, upper end of Lake Austin, 1946, M. Wheeler et al. 16T229 (TEX); seepage along upper Bull Creek, 1946, J. Adamcik & F. A. Barkley 16T205 (F, GH, TEX); hills W of Austin, Common Ford Rd. ca. 1 mi. N of Bee Cave Rd. (Rt. 2244), 1983, B. Ertter & M. Baker 4816 (CAS, NY, WIS); North Cat Mountain, N of Valburn Drive from Valburn Circle N., 1991, R. Kral & S. Jones 78655 (MO, TENN); Colorado River, Austin, 1936, B. C. Tharp s.n. (CAS); west of Austin near Beecaves, 1941, C. L. & A. A. Lundell 10289 (LL); Travis [Trinity?] Co., Onion Creek, 1930, B. C. Tharp s.n. (F, GH, NY, UC); Williamson Co., 1946, E. J. Dyksterhuis et al. s.n. (TEX); Wise Co., Denton-Decatur Rd., 1940, C. L. & A. A. Lundell 8461 (LL, MICH).

4a. *Eleocharis compressa* Sullivant, Amer. J. Sci. 42: 50. 1842; var. ***compressa***. *Eleocharis elliptica* Kunth var. *compressa* (Sullivant) Drapalik & Mohlenbrock, Amer. Midl. Naturalist 64: 20. 1960. TYPE: U.S.A. Ohio: wet places in the Darby Plains, 15 mi. W of Columbus, 1840?, W. S. Sullivant s.n. (holotype, NY; isotype, WIS).

The holotype is a complete specimen including a clearly visible scaly rhizome similar to that of *E. compressa* var. *acutisquamata* (Fig. 3D). The floral scale apices are clearly bifid (Fig. 1A), not simply split during development or lacerated by wear. Because the apices of the proximal scales of the spikelet are worn or hidden underneath the mounted spikelets, their form is not clearly observable. There is only one achene on the holotype and several on the isotype at WIS. There are also four possible isotypes at NY.

The type fits Sullivant's description in the protologue of *E. compressa* as having "deeply 2-cleft" floral scale apices. Later authors, however, stated that the scales are "commonly bifid" (Svenson, 1932, 1957) or only "lacerate in age" (Gleason, 1968). My observations of specimens that Svenson assigned to *E. compressa* show that the floral scale apices vary from all deeply bifid to all entire, often in the same spikelet (see Fig. 1A).

The earlier name *Eleocharis acuminata* (Muhlberg) Nees [in *Linnaea* 9: 294 (1834), basionym *Scirpus acuminatus* Muhlenberg in *Descr. Gram.*: 27 (1817)], was given as a synonym of *E. compressa* in *Index Kewensis* (Trustees of the Royal Botanic Gardens, Kew, 1: 829 and version 2.0 (1997)) as well as in several later databases (TROPICOS, Missouri Botanical Garden, 2001; International Organization for Plant Information, 2000; USDA, NRCS, 2001; *Synthesis of the North American Flora* [but questioned with ?], Kartesz & Meachum, 1999), but it should be treated as a *nomen confusum* pending further study and typification (Svenson, 1932: 217).

Eleocharis compressa and *E. acutisquamata* Buckley are here combined because they constitute a single, morphologically extremely variable complex within which species cannot be clearly distinguished. *Eleocharis compressa* var. *compressa* (Fig. 1A–E) as here defined differs from *E. compressa* var. *acutisquamata* (Fig. 3A–D) mainly in the cross-section shape (and width) of the culms, which are about 2–5× as wide as thick and 0.5–1.8 mm wide in *E. compressa* var. *compressa*, but terete to about twice as wide as thick and 0.2–1 mm wide in *E. compressa* var. *acutisquamata*. *Eleocharis compressa* var. *compressa* is known mainly from the tall-grass prairie region, whereas *E. compressa* var. *acutisquamata* is known mainly from farther west in the Great Plains.

In the specimens that Svenson identified as *E. compressa* or *E. acutisquamata*, the floral scale apices vary from all deeply bifid to all entire as well as from narrowly attenuate to merely acute; the culms vary from all terete to some or all distinctly compressed; the styles are often trifid and bifid in the same spikelet; and the achenes vary from nearly equilaterally trigonous to biconvex, often in the same spikelet. This variation strongly suggests hybridization with *E. erythropoda* (as reported from Ontario by Catling, 1994), *E. elliptica*, *E. macrostachya*, and perhaps *E. montevidensis*, which are all partly sympatric with *E. compressa*. I have observed putative *E. compressa* × *elliptica* and *E. compressa* × *erythropoda* hybrids in calcareous fens and degraded wet prairies in southeastern Wisconsin.

4b. *Eleocharis compressa* var. *acutisquamata* (Buckley) S. G. Smith, stat. nov. Basionym: *Eleocharis acutisquamata* Buckley, *Proc. Acad. Nat. Sci. Philadelphia* 1862: 10. [1863.] TYPE: U.S.A. Texas: San Saba Co., Buckley s.n. (holotype, PH).

The label on the type reads only "E. acutisquamata Buckl. San Saba," which is on the Edwards Plateau ca. 80 mi. NW of Austin. The type consists of a single tuft with about 2 mm of rhizome and several fruiting spikelets. Its culms are subterete, mostly with ca. 5 to 6 blunt ridges when dry. Most floral scales are acuminate and entire, with a few shallowly bidentate. The type is similar to many specimens I have identified as *E. compressa* var. *acutisquamata*.

In his 1863 protologue Buckley described *E. acutisquamata* as having culms filiform (thus presumably more or less terete) and scales acute. The type fits this description except that most floral scale apices are attenuate, and the scales in about the proximal half of the spikelet are shallowly bidentate. Svenson (1957) described the scale apices as "acute to acuminate," and Correll and Correll (1972) described them as "long-attenuate sometimes bifid (split) acute."

Index Kewensis [Jackson, 1893, 1: 830] erroneously gave *E. acutisquamata* as a synonym of *E. palustris*.

The unpublished chromosome count of "n = 12; 2n = 24 (taken from mitotic MC)" that is given on the label on the following specimen of *E. compressa* var. *acutisquamata* is the only count for *E. compressa* that I have verified by a voucher: U.S.A. Kansas: Trego Co., Cedar Bluff Reservoir, sandy lake shore, 16 June 1964, L. J. Harms 2419 [labeled *E. compressa*] (KANU).

C. *ELEOCHARIS* SUBGENUS *ZINSERLINGIA* T. V. EGOROVA

Eleocharis subg. *Zinserlingia*, segregated from series *Pauciflorae* Svenson (1929), is amply distinct from other groups of *Eleocharis* and is probably monophyletic (Gonzalez-Elizondo & Peterson, 1997; Gonzalez-Elizondo et al., 1997; Roalson & Friar, 2000). It is technically defined mainly by the proximal internodes of the rachillae thicker and shorter than internodes in the middle of the spikelet, whereas in the rest of the genus the internodes are all about the same thickness and length. All of the North American species are very similar in both vegetative and sexual reproductive characters. The group ranges widely in North America and Eurasia and is disjunct in the Andes of temperate South

America. It comprises perhaps eight species and is much in need of a worldwide taxonomic revision. I recognize the following four species for North America: (1) *E. quinqueflora* (F. X. Hartman) O. Schwarz; (2) *E. suksdorfiana* Beauverd [= *E. quinqueflora* var. *suksdorfiana* (Beauverd) Hultén]; (3) *E. bernardina* (Munz & I. M. Johnston) Munz & I. M. Johnston [= *E. quinqueflora* var. *bernardina* (Munz & I. M. Johnston) Gonzalez-Elizondo & P. M. Peterson]; (4) *E. torticulmis* S. G. Smith (described herein). The characteristics of these species are summarized in Table 1.

Eleocharis quinqueflora was long known as *E. pauciflora* (Lightfoot) Link (described from Scotland) until O. Schwarz [in Mitt. Thüring. Bot. Ges. I: 89. 1949] adopted the name *E. quinqueflora* (also described from Europe) without explanation. Svenson (1929: 380) described *E. pauciflora* var. *fernaldii* for eastern North American plants mainly on the basis of less robust, softer plants, "scarcely indurated" caudices, and small differences in achenes and perianth bristles. Löve [in Svensk Bot. Tidskr. 48: 1: 380. 1954] raised variety *fernaldii* to species status because his chromosome count of $2n = 80$ was lower than counts of $2n = \text{ca. } 100$ from Europe. Both *E. suksdorfiana* (1921) and *E. bernardina* (1925) were first described from North America as species. They were both reduced to varieties of *E. pauciflora* by Svenson (1934) because of perceived morphological intergradation, and later Svenson (1957) listed them as synonyms without comment. Hultén (1958) and Meusel et al. (1965) provided maps of *E. quinqueflora* s. str. (under *E. pauciflora*) and varieties for the Northern Hemisphere; they treated typical *E. pauciflora* as circumboreal and recognized *E. pauciflora* vars. *fernaldii* and *suksdorfiana* in North America as well as three other varieties in Eurasia. Hultén [in Ark. Bot. (n.s.) 7: 1: 24. 1968] and J. T. Howell [in Marin Flora, ed. 2, suppl.: 363. 1969] transferred *E. pauciflora* var. *suksdorfiana* to *E. quinqueflora* without comment, and Gonzalez-Elizondo and Peterson (1997) treated *E. bernardina* as *E. quinqueflora* var. *bernardina* because of perceived morphological intergradation.

As thus broadly defined *E. quinqueflora* is morphologically extremely variable. In contrast, my studies have shown that when different characters are used there are distinct morphological discontinuities, and four distinct species can be recognized for North America.

Eleocharis quinqueflora is circumboreal. In North America it includes *E. quinqueflora* subsp. *fernaldii* (Svenson) Hultén and two or three other undescribed intergrading variants that may deserve taxonomic recognition. Recognition of infraspecific taxa is premature pending a taxonomic revision of subgenus

Zinserlingia. Although not mentioned in major European floras (Schulze-Motel, 1967; Walters, 1980), enlarged terminal overwintering buds, herein termed bulbs, that are similar to those commonly formed by North American plants were described and illustrated for Scandinavia by Strandhede and Dahlgren (1967) as typical of *E. quinqueflora*. These bulbs have fleshy food-storage modified leaves and tunicating papery scales, and plants that develop from them have bulbous culm-tuft bases with tunicating papery scales. Plants that form bulbs also lack hard, thick caudices. Pending a worldwide taxonomic revision, for North America I have assumed that the ability to produce bulbs and bulbous culm-tuft bases is characteristic of *E. quinqueflora* (see Table 1). With rare exceptions North American plants of *E. quinqueflora* also have a flower in the axil of the proximal scale of the spikelet.

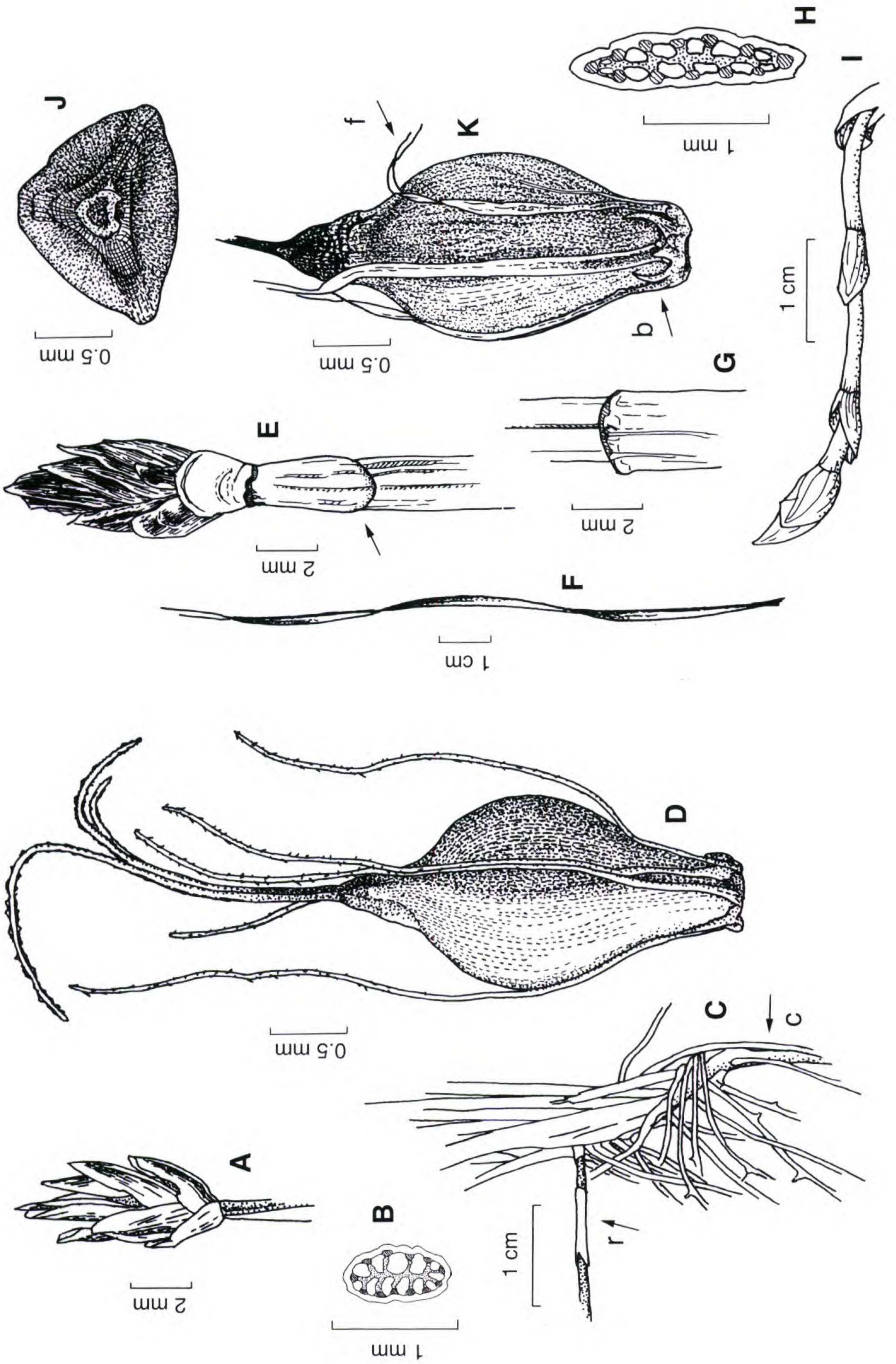
Eleocharis suksdorfiana, *E. bernardina*, and *E. torticulmis* are clearly closely related. They all differ from *E. quinqueflora* as here defined in the presence of well-developed caudices and the lack of underground bulbs or bulbous culm-tuft bases (see Table 1). Except for a few specimens of *E. suksdorfiana* these species also almost always lack a flower in the axil of the proximal scale. Based on my study of many specimens, including isotypes at GH, ISC, NY, and UC, I herein define *E. suksdorfiana* (see Table 1) differently from Svenson (1934) and Gonzalez-Elizondo et al. (1997), both of whom included plants with unusually large, ovoid bulbs. I place these large-bulbed plants in *E. quinqueflora*. Beauverd's (1921) fairly complete description closely matches the isotypes and all specimens I have identified as *E. suksdorfiana*, which is widely but locally distributed in western North America from near sea level to ca. 3300 m. *Eleocharis bernardina* is clearly closely related to *E. suksdorfiana* but differs qualitatively in several vegetative and perianth bristle characters as given in Table 1. It is very local in southern California.

A few specimens from a small area in northeastern California are clearly closely related to *E. suksdorfiana* and *E. bernardina* but consistently differ from them in several vegetative and perianth bristle characters (see Table 1). These specimens are described as a new species as follows:

1. ***Eleocharis torticulmis*** S. G. Smith, sp. nov.
 TYPE: U.S.A. California: Plumas Co., Northern Sierra Nevada, Crescent Mills Quadrangle, T25N R9E NE 1/4 SE1/4 sec. 20, N40°00'47", W120°59'28", Sweetwater Meadow in Butterfly Valley Botanical Area, *Darlingtonia* fen, elev. 1177 m, 3 July 2000, L. P. Janeway & B. Castro 6874 (holotype, JEPS; isotypes, CHSC, GH, MO, NY, OSC, RSA, US, WIS). Figures 2, 4.

Table 1. Distinguishing characteristics of the North American species of *Eleocharis* subg. *Zinserlingia*.

| | <i>E. quinqueflora</i> | <i>E. bernardina</i> | <i>E. suksdorfiana</i> | <i>E. toriculmis</i> |
|--|--|---|--|--|
| Rhizome thickness | 0.2-1 mm | 0.5-1 mm | 0.5-1.5 mm | 1.5-2 mm |
| Underground and basal bulbs | often present | absent | absent | absent |
| Caudices | absent or soft, to 0.5 mm thick | present, hard, 1-2 mm thick | present, hard, 1-2 mm thick | present, hard, 3 mm thick |
| Culm tuft bases | often bulbous and tunicated with scales | never bulbous or tunicated with scales | never bulbous or tunicated with scales | never bulbous or tunicated with scales |
| Culm habit | erect, not spirally twisted | markedly arched, not spirally twisted | erect, not spirally twisted or slightly so | erect, markedly spirally twisted |
| Culm cross section | subterete to slightly compressed, to ca. 2× wider than thick | subterete to slightly compressed, to ca. 2× wider than thick | subterete to slightly compressed, to ca. 2× wider than thick | greatly compressed, ca. 3-4× wider than thick |
| Culm width | 0.2-0.5 (-1.2) mm | 0.5-1 mm | 0.5-1.2 mm | 1.5-2.5 mm |
| Culm contraction | not contracted | not contracted | not contracted | obliquely contracted proximal to spikelet |
| Proximal scale flower | absent or rarely present | absent | absent or rarely present | absent |
| Perianth bristle number | ca. 3-6 | ca. 4-7 | 6 | 1 to ca. 5 or apparently absent |
| Perianth bristle dimensions and indument | variable, often unequal, rudimentary to equaling tubercle, stout to slender, smooth to densely spinulose | unequal, less than half of to equaling achene, the shorter stout, smooth, the longer slender, densely spinulose | about equal, the longest equaling achene to exceeding tubercle, all slender, densely spinulose | unequal, rudimentary to ca. equaling achene, the shorter stout, smooth or nearly so, the longer slender, densely spinulose |
| Achene dimensions | 1.6-2.3 × 0.7-1.3 mm | 1.5-2.1 × 0.9-1.2 mm | 1.7-2.3 × 0.7-1.3 mm | 1.7-2.8 × 1-1.3 mm |
| Elevation | ca. 0-3600 m | 2100-2700 m | ca. 10-3300 m | 1200 m |
| Distribution | Circumboreal | Southern California | Western North America | Northeastern California |



Species *E. suksdorfiana* Beauverd affinis sed rhizomatibus 1.5–2 mm crassis, caudicibus 3 mm crassis, culmis tortis valde compressis magnopere 3–4-plo latis quam crassis contractis oblique circa 5 ad 40 mm spiculis proxime, perianthiis setis 3 brevissimis ad dimidium fructus interdum 1 vel 2 ad circa aequantibus tuberculis differt.

Perennial, 20–40 cm. *Rhizomes* ca. 7 cm × 1.5–2 mm; internodes ca. 1–2 cm; soft; cortex breaking loose, papery; central cylinder firm, tough; apical buds not enlarged or becoming bulbous, bulbs absent; scales ca. 7–9 mm, thinly papery, sometimes fibrous in age. *Scales (prophylls) among culm bases* brown, long-ovate, acute, ca. 13–20 × 6 mm, papery, often fibrous. *Caudices* vertical or ascending, short, hard, obscured by dead remains of culms, scales, and roots, ca. 3 mm thick. *Culms* in small tufts; tuft bases never bulbous or tunicated with scales; erect; markedly spirally twisted; obliquely contracted ca. 5–40 mm proximal to spikelet; greatly compressed, 1.5–2.5 mm wide, ca. 3–4× wider than thick when fresh; firm; nearly smooth or with up to 6 broad, rounded ridges on each side when dry, at 15–20× with many very fine ridges. *Proximal leaf sheaths* distally disintegrating, membranous-hyaline. *Distal leaf sheaths* persistent, not splitting ventrally, stramineous to gray or brown; papery; summits dark brown to reddish, subtruncate, ventrally truncate to shallowly concave, sometimes callose, apex broadly obtuse, without a tooth-like rudimentary blade. *Spikelets* terete, oblong, acute to rounded, 6–8 × 2–3 mm. *Proximal scale* without a flower, amplexicaulous, broadly oval, entire, ca. 3–4 mm, mostly hyaline and colorless, proximally ca. 0.5–1 mm green or brown with dark brown margin and callose. *Subproximal scale* with a flower. *Floral scales* spiraled, appressed in fruit, ca. 8 to 10, ca. 2 per mm of rachilla; bright medium to chestnut brown or partly stramineous; oblong-ovate, apices rounded to acute, entire; 4–5.5 × ca. 2 mm; membranous; margins and apices very narrowly colorless and hyaline or like flanks; midrib obscure or evident. *Perianth bristles* 1 to ca. 5 or apparently absent, brown to stramineous, very unequal in same flower, 0.2–2.5 mm, the shorter stout, smooth or sparsely spinulose, the longer slender, densely spinulose, the spinules spreading, sharp to blunt, about as long as bristle width. *Stamens* 3,

anthers pale yellow, thecae 1.8–3.0 × ca. 0.3 mm; connective extension brown, 0.5 mm, blunt to acute. *Styles* trifid about half of their length, ca. 6–8 mm, stigmas puberulent. *Tubercles* confluent with achene, usually clearly different from achene in color and texture, dark brown to stramineous, pyramidal, 0.25–6 × 0.3–0.55 mm. *Achenes* persistent with scales; stramineous to medium brown; obpyriform; thickly trigonous, angles prominent, rounded; ca. 1.75–2.75 mm long × 1.25 mm wide; usually distally narrowed into a stout beak that is stramineous to pale brown and ca. 0.3–0.6 mm long; usually finely reticulate at 10–20×, clearly to obscurely finely longitudinally ridged.

Distribution and ecology. *Eleocharis torticulmis* is known only from the type locality and immediate vicinity in Plumas Co., California (Fig. 2). Knight et al. (1970: 1–4) described the general ecology of the area in which the few collections have been made. All collections are from open wet meadows in mixed-conifer (mainly *Pinus ponderosa*) forest in the Arid Transition Zone at ca. 1180 m in the northern Sierra Nevada. Paleozoic marine sedimentary and metamorphic rocks dominate the area, rather than granite, which dominates the Sierra Nevada to the south, or volcanic rocks of the mountains a short distance to the north. Documents obtained by L. Janeway from the Plumas National Forest state that the 5-acre Butterfly Valley Botanical Area has folded metamorphic sedimentary and volcanic interlayered rock, and that groundwater and soil chemistry suggest a serpentine influence. Serpentine-based soils occur 3–4 miles to the west. As there are many serpentine-endemic plant species in California it is possible that *E. torticulmis* is endemic to serpentine soils.

The known habitat is gently sloping very wet to fairly dry places in spring-fed meadows, usually with a thin layer of sluggish sheet-flow water. At the type locality *E. torticulmis* was codominant in the peripheral parts of the meadow with *Rhynchospora capitellata* (Michaux) Vahl, *Hastingsia alba* (Durand) S. Watson, and *Juncus oxymeris* Engelman, while *Darlingtonia californica* Torrey was dominant in the central part of the meadow with *Hastingsia alba*, *Nartheicum californicum* Baker,

←

Figure 4. A–D, *Eleocharis suksdorfiana* Beauverd. —A. Spikelet. —B. Culm cross section. —C. Proximal part of culm tuft with part of caudex (c) and part of rhizome (r). —D. Achene with perianth bristles. E–I, *Eleocharis torticulmis* S. G. Smith. —E. Spikelet with part of culm showing oblique contraction (arrow). —F. Portion of culm, habit. —G. Distal leaf sheath summit. —H. Culm cross section. —I. Rhizome. —J, K. Achenes with stamen filaments (f) and very short perianth bristles (b). A, drawn from Tracy 14220 (UC); B and D, drawn from Janeway et al. 2499 (CHSC); C, drawn from Oswald & Ahart 4793 (CHSC); E and G and I to K, drawn from Janeway & Castro 6874 (TYPE); F, drawn from Knight et al. 1772 (NY).

Tofieldia occidentalis S. Watson, and a little *E. torticulmis*. At the site of the Ahart 8383 paratype, *E. torticulmis* was dominant in a wide band of very wet meadow around the pond extending to the dry margin of the pine forest, with scattered *Hastingsia alba*, *Carex echinata* Murray, and *Juncus oxymersis*. At the pond the dominance by *E. torticulmis* rapidly changes to dominance by *Carex vesicaria* L. At the upper edge of this very wet meadow, *E. torticulmis* occasionally gives way to more *Juncus oxymersis*, *Helenium bigelovii* A. Gray, *Mimulus primuloides* Benth, *Platanthera sparsiflora* (S. Watson) Schlechter, and *E. suksdorfiana* (*E. suksdorfiana* vouchers: Janeway & Castro 6875 (CHSC), L. Ahart 8384 (CHSC), J. Battagin s.n. (CHSC), W. & I. Knight & T. Howell 1537 (CAS)). At the only other meadow where *E. torticulmis* has been found, 1.1 km north of Butterfly Valley (Janeway & Castro 6876 paratype), there is no standing water; *E. torticulmis* is almost hidden by the dominant *Juncus oxymersis*, and *Carex lemmonii* W. Boott, *C. feta* L. H. Bailey, *Triteleia hyacinthina* (Lindley) Greene, and *Sisyrinchium bellum* S. Watson are also common. The W. & I Knight 1339 paratype of *E. torticulmis* from Butterfly Valley, however, is labeled "dry vernal area."

The collections made in 1966 bear very few mature achenes or flowers with anthers. The collections made in 2000 bear many mature achenes and flowers with exerted anthers, and many spikelets contain mature achenes proximally and flowers with exerted anthers distally. The more recent collections also bear actively growing rhizomes with apical buds forming new aerial shoots. No underground bulbs are known; overwintering is presumably by means of buds concealed among the culm bases and scales of the aerial shoots and caudices as in *E. suksdorfiana* and *E. bernardina*. Several of the specimens Knight et al. (1970) identified as *E. suksdorfiana* are *E. torticulmis*.

Eleocharis suksdorfiana differs from *E. torticulmis* consistently and qualitatively as follows (see Table 1): *Rhizomes* 0.5–1.5 mm thick; sprouting apical buds enlarged, ellipsoid, ca. 10 × 2–5 mm. *Caudices* ca. 1–2 mm thick. *Culms* erect; terete to slightly compressed, 0.5–1.2 mm wide, to ca. 2× wider than thick; slightly or not spirally twisted; not contracted subproximal to spikelets. *Perianth bristles* 6, all slender and spinulose, about equal, the longest about equaling the achene to exceeding tubercle. Widespread, ca. 10–3300 m elevation. *Eleocharis bernardina* differs from *E. torticulmis* consistently and qualitatively as follows (see Table 1): *Rhizomes* ca. 0.5–1 mm thick. *Caudices* ca. 1–2 mm thick. *Culms* strongly arched, not spirally

twisted, not contracted subproximal to spikelets. *Perianth bristles* ca. 4 to 7, less than half of to equaling achene, the shorter stout, smooth, the longer slender, densely spinulose. Very local in southern California at 2100–2700 m.

The epithet *torticulmis* describes the markedly spirally twisted culms.

Paratypes. U.S.A. **California:** Plumas Co., head of small drainage to East Branch North Fork Feather River from the SE, vicinity of Paxton, ca. 1.1 km N of Butterfly Valley Botanical Area, open meadow with wet clayey soil but no water on the surface, with *Juncus oxymersis* dominant and *Carex lemmonii*, *C. feta*, *Triteleia hyacinthina*, and *Sisyrinchium bellum* also present, 3 July 2000, L. P. Janeway & B. Castro 6876 (CAS, CHSC, MICH, NMSC); by small stream in bog, ca. 150 feet NW of pond, Butterfly Valley, ca. 5 air mi. NW of Quincy, bog in yellow pine forest, elev. 3300 ft., 21 May 2000, L. Ahart 8383 (CHSC, JEPS, WIS); Butterfly Valley, near Pond Reservoir, 18 June 1966, W. & I. Knight 1339 (CAS); Butterfly Botanical Area and vicinity, dry vernal area, Pond Reservoir, elev. 3600 ft., 26 July 1966, W. & I. Knight & T. Howell 1394 (CAS); in profusion at north end of Pond Reservoir, elev. 3600 ft., 28 July 1966, W. & I. Knight & T. Howell 1524 (CAS); Sweetwater Meadow, 28 July 1966, W. & I. Knight & T. Howell 1672 (CAS, NY); Sweetwater Meadow in Butterfly Valley Botanical Area, *Darlingtonia* fen (type locality), 13 Sep. 2000, L. P. Janeway et al. 6969 (CHSC, JEPS, US); by little creek in Pond Meadow, 17 June 2000, J. Battagin s.n. (CHSC).

D. *ELEOCHARIS* SUBGENUS *SCIRPIDIUM* (NEES) KUKKONEN

Eleocharis subg. *Scirpidium* is comprised of about 12 species from Eurasia, North America, and South America. Although delimitation of species is sometimes difficult, this group is less troublesome than the other groups discussed herein. *Eleocharis acicularis* is circumboreal and quite variable. At first Svenson (1929) recognized four varieties and two forms in North America but later (1957) did not recognize infraspecific taxa. Most of the plants found within the regions of Pleistocene glaciation are very similar to typical *E. acicularis* (culms cylindrical or 3- or 4-angled (see Fig. 5), distal leaf sheaths mostly obscure, tubercles about as high as wide, achenes about 2× longer than wide). South of the glaciated region, however, many plants have been placed in *E. acicularis* var. *occidentalis* Svenson (distinguished by plants only 2–8 cm tall, culm tuft bases often swollen, cormous, culms often 6- to 8-ribbed, distal leaf sheath summits often evident, inflated, tubercles usually depressed, achenes less than 2× longer than wide), and a few in *E. acicularis* var. *gracilescens* Svenson (distinguished by plants often tall, to 22 cm, culms smooth or sometimes finely 5- to 12-ribbed, spikelets often linear-lanceolate, 4–8 mm long, floral scales often

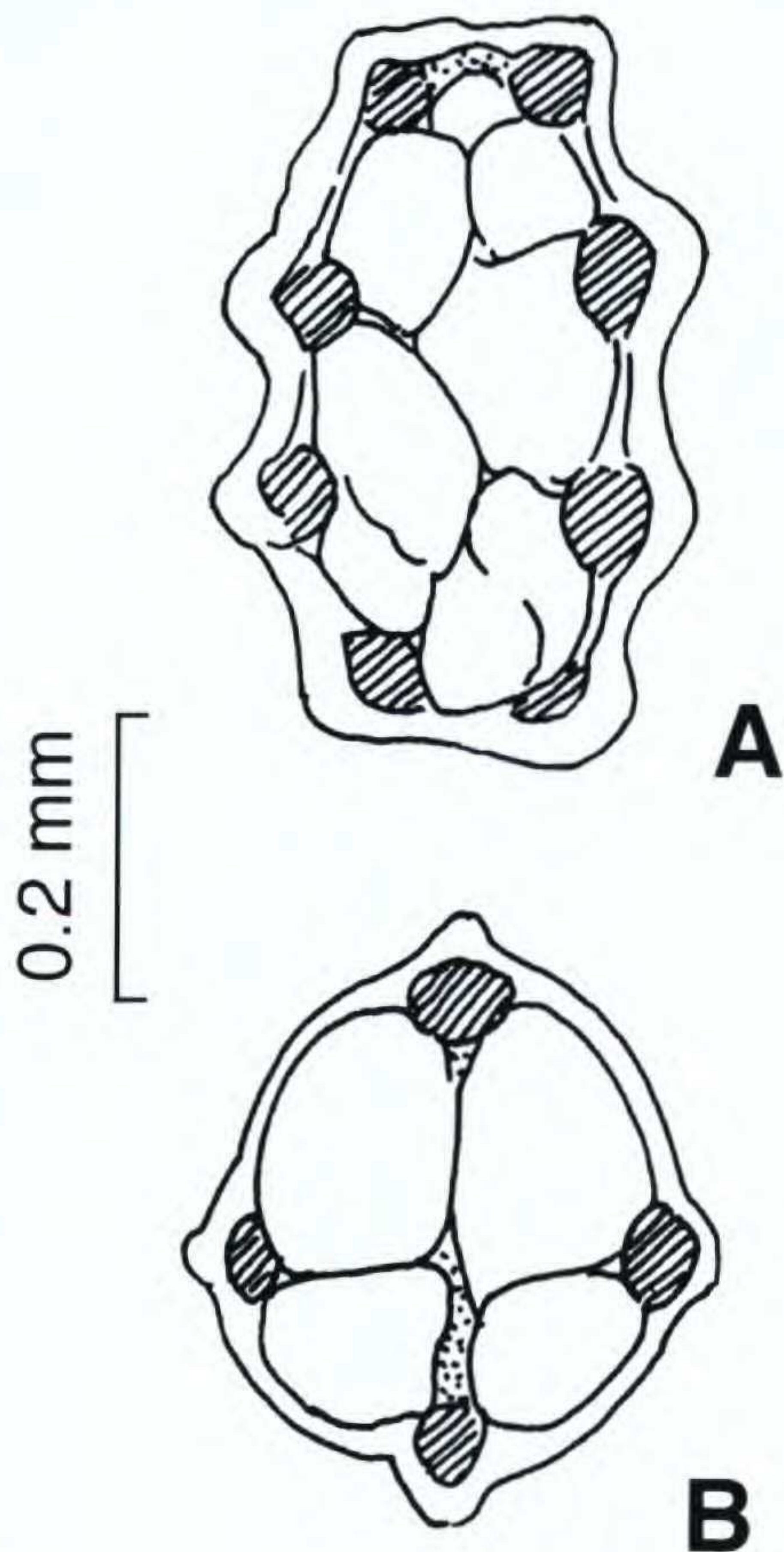


Figure 5. Culm cross sections. —A. *Eleocharis acicularis* (L.) Roemer & Schultes var. *porcata* S. G. Smith. —B. *Eleocharis acicularis* var. *acicularis*. A, drawn from Correll & Correll 39584 (UC); B, drawn from Fraser 493 (KSC).

stramineous, 2.5–3.5 mm long, achenes less than 2× longer than wide).

Some plants of *E. acicularis*, mostly from the Great Plains, do not fit any described variety. Because of their compressed, prominently ridged culms, these plants, including a paratype of *E. wolfii* (Illinois, 1861, *Elihu Hall s.n.*, GH), are sometimes misidentified as *E. wolfii*. The Hall collection was originally mounted on the same sheet as the holotype (Illinois, 1874, *John Wolf s.n.*, GH) of *E. wolfii*, but it was later separated along with a single tuft of *E. wolfii* (part of the type collection?) by cutting the sheet and filed in the general collection. In 1928 Svenson overlooked the several tufts of *E. acicularis* on the segregated sheet and annotated the Hall collection as *E. wolfii*. These confusing plants are here described as a new variety based primarily on their prominently ridged culms:

1. *Eleocharis acicularis* (L.) Roemer & Schultes var. *porcata* S. G. Smith, var. nov. TYPE: U.S.A. Texas: Dawson Co., playa 7 mi. W of Lamesa, near intersection of Farm Rd. 829 with U.S. 180, in clumps in mud, 9 May 1966, *D. S. Correll* 32796 (holotype, NY; isotypes, KANU, LL). Figure 5.

Varietas ab *E. acicularis* var. *acicularis* foliis vaginis distalis apicibus persistentibus firmis, culmis plerumque manifeste compressis 6–12-porcatis differt; ab *E. acicularis* var. *occidentalis* Svenson culmis basibus non tumidis, fructibus brevioribus differt.

Plants to ca. 22 cm tall. *Culms* 0.2–0.5 mm wide, at least some prominently 6- to 12-ridged, mostly distinctly compressed, usually firm, their bases not persistent and corm-like. *Distal leaf sheath summits* persistent, firm, usually inflated. *Spikelets* 3–7 mm long. *Floral scales* (1.5–)2–2.5 mm, flanks mostly bright orange-brown. *Perianth bristles* absent [rarely a few present?]. *Tubercles* depressed, ca. 0.05–0.1 long × 0.15–0.25 mm wide. *Achenes* less than 2× longer than wide, ca. 0.65–0.85 long × 0.5 mm wide, “neck” lacking (thus tubercle sessile).

Distribution and ecology. *Eleocharis acicularis* var. *porcata* is known from scattered localities in Canada: Alberta; and U.S.A.: Colorado, Illinois, Kansas, Nebraska, North Dakota, New Mexico, Texas, and Wyoming; at elevations from near sea level to at least 2200 m. Reported habitats are mud and very shallow water of fresh marshes, ponds, stream margins, prairie depressions, and ditches. Flowering and fruiting are from April (in southern Texas) to August.

This variety differs from all other known *E. acicularis* except variety *occidentalis* in the usually distinctly compressed culms, at least some culms on each plant with 6–12 prominent ridges (Fig. 5). It differs from variety *E. acicularis* var. *occidentalis* in its shorter achenes (0.85–1 mm in var. *occidentalis*) and the culm bases not persistent and corm-like. It morphologically intergrades with the other three varieties.

The epithet *porcata* describes the prominently ridged culms.

Paratypes. CANADA. **Alberta:** Bow River near Eau Claire sawmills, Calgary, 1948, *W. C. McCalla* 10289 (ALTA); Stettler Area, Paintearth, 1974, *A. Klar* 483 (ALTA); river near Kinninvic, 1927, *E. H. Moss* 1184 (ALTA, NDA). U.S.A. **Arizona:** Cocconino Co., marsh below Black Spring, 7 mi. S of Flagstaff, 1966, *J. R. Crutchfield* 1965 (NY); Cochise Co., Cooley’s Ranch, 1912, *L. N. Gooding* 1107 (NY). **Colorado:** Lincoln Co., 7 mi. S of Hall Station, 1937, *M. Ownbey* 1321 (DS, GH, WTU); Weld Co., Ephemeral pond, Pawnee Natl. Grassland near Murphey Reservoir, 1995, *D. L. Hazlett* 9168 (NY); Yuma Co., wheat field 2.5 mi. E of Yuma, 1973, *S. Stephens* 65530 (KANU). **Illinois:** 1861, *E. Hall s.n.* (GH). **Kansas:** Cloud Co.: N of Jamestown, 1938, *S. V. Fraser* 493, (KSC); Saline Co., Ditch, Colby Branch Railroad N of Salina, 1943, *John Hancin* 2448 (KSC); ditch, railroad N of Mulberry Creek bridge, 1931, *J. Hancin* 950 (KSC). **Louisiana:** Tangipahoa Pa., railroad, Hammond, 1969, *C. J. Kirby* 52 (LSU). **Nebraska:** Chase Co., prairie depression near Lamar, 1942, *W. L. Tolstead* 9925 (BRIT) [det. *E. wolfii*]; Hamilton Co., 6 mi. W of Aurora, 1944, *W. Keiner*

16770 (GH); Kearney Co., Minden, 1897, *H. Hapeman s.n.* (NMC). **New Mexico:** Colfax Co., vicinity of Ute Park, 1916, *P. C. Standley 13931* (GH); San Miguel Co., in 2–3 inches water, Laguna Huerfana, 8 mi. NW of Trujillo, 1965, *J. R. Crutchfield 418* (LL); 18 mi. E of Las Vegas, 1982, *S. R. Hill & P. -A. Levandoski 12043* (GH); Crystal Pasture, 9.5 mi. W of Trujillo, 1982, *S. R. Hill & A. D. Cress 1168* (GH). **North Dakota:** Burke Co., road ditches and farmland between Portal and Northgate road, 1969, *G. D. Hegstad 1398* (NDA); Mountrail Co., prairie, road ditch and slough S of Lower Lostwood Reserve, 1970, *G. D. Hegstad 5555* (NDA). **Texas:** Cameron Co., 20 mi. N of Brownsville, 1944, *Runyon 3679* (TEX); Wichita Co., Wichita Falls, 1926, *L. M. Kee 9158* (NY).

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Appendix. Extract from letter from H. K. Svenson to H. H. Iltis (5 May 1966): "I am returning the specimens

of *Eleocharis*, chiefly from Wisconsin. As I surmised, this fine collection of material might well have solved the troublesome problem of the relationships of *Eleocharis compressa* and *E. elliptica*, and it has done so to my satisfaction. My error lay in placing too much emphasis on the flattened stem structure of the Great Lakes material. What I called *E. compressa* var. *atrata* I now feel confidently should be placed under *E. elliptica*. Whether these culms are truly ancipital in the sense of *E. compressa* I now have my doubts. . . .

The achenes, including tubercle, were correctly portrayed by me in *Rhodora* 34: Pl. 219, fig. 61 and 63. 1932. I have collected good material of *E. acutisquamata* in Texas, and it should be included under *E. compressa*. In *Rhodora* 34: plate 221, the correct achene is shown as a photograph. I am not certain about fig. 5, of the same plantplate, and suspect some error may have crept in. The achene of *E. compressa* is very fine-meshed as compared with *E. elliptica*; the color is olive [i.e. yellow-brown] as contrasted with the deep yellow of *E. elliptica*; the achenes are a little narrower in *E. compressa*, and generally lack the corrugation of surface seen in *E. elliptica*. The scales of *E. compressa* are also firmer, with a consistency much as in eastern *E. smallii*. . . ."