INFRASPECIFIC TAXONOMY AND NOMENCLATURE OF
ELEOCHARIS ACUTANGULA (CYPERACEAE)

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ABSTRACT
A taxonomic study of Eleocharis acutangula (Roxb.) Schult. was conducted in order to better define this poorly understood and variable pantropical species. Multivariate statistical analysis, and ecological and distributional data of worldwide collections of E. acutangula provided the basis for its segregation into E. acutangula subsp. acutangula, E. acutangula subsp. breviseta D.J. Rosen, subsp. nov., and E. acutangula subsp. neotropica D.J. Rosen, subsp. nov. Nomenclatural research necessitated the lectotypification of E. acutangula and a heterotypic synonym, E. fistulosa Schult. var. robusta Boeck. A taxonomic treatment of E. acutangula is provided that includes a key to the subspecies, detailed descriptions, illustrations, and notes on habitat and distribution.

RESUMEN
Se realizó un estudio taxonómico de Eleocharis acutangula (Roxb.) Schult. para definir mejor esta especie pantropical variable y pobremente conocida. Un análisis estadístico multivariante, y datos ecológicos y de distribución a nivel mundial de E. acutangula fueron la base para su segregación en E. acutangula subsp. acutangula, E. acutangula subsp. breviseta D.J. Rosen, subsp. nov., y E. acutangula subsp. neotropica D.J. Rosen, subsp. nov. La investigación nomenclatural precisó la lectotipificación de E. acutangula y de un sinónimo heterotípico, E. fistulosa Schult. var. robusta Boeck. Se aporta un tratamiento taxonómico de E. acutangula que incluye una clave de subespecies, descripciones detalladas, ilustraciones, y notas sobre el hábitat y distribución.

Eleocharis R. Br. is a cosmopolitan genus of about 200 species and over 600 published names with a center of diversity in the Neotropics (González-Elizondo & Tena-Flores 2000). Eleocharis subg. Limnochloa (P. Beauv. ex Lestib.) Torr. (= Eleocharis sect. Mutatae Svenson) comprises over 35 species occurring in seasonally wet to permanently flooded habitats from principally tropical regions, and is distinguished from other Eleocharis by a combination of the following morphological characteristics: (1) cartilaginous, un-keeled (rarely obscurely-keeled), many-veined floral scales; (2) generally large culms that are often as thick as the cylindrical spikelet; and (3) biconvex (rarely trigonous) achenes usually with epidermis of large, conspicuous polygonal cells (Svenson 1929; González-Elizondo & Peterson 1997). Five new species in subg. Limnochloa have recently been described from the New World: E. eglerioides S. González & Reznicek and E. liesnerii S. González & Reznick from Venezuela (S. González-Elizondo & Reznicek 1996), E. yecorensis Roalson from Mexico (Roalson 1999), E. laeviglumis R. Trevis. & Boldrini from Brazil (Trevisan & Boldrini 2006), and E. steinbachi D.J. Rosen from Bolivia (Rosen & Hatch in press). However, no comprehensive study of subg. Limnochloa has been published since the seminal work of Svenson (1929, 1939).

Eleocharis acutangula (Roxb.) Schult. is the most widely distributed species of Eleocharis subg. Limnochloa (Svenson 1939 [as E. fistulosa Schult.]). In the New World it is reported from near sea level to elevations over 2200 m from various habitats including cloud forests, forest depressions, savannahs, grasslands, palm swamps, lake margins, borrow pits, and roadside ditches. Old World habitats include swamps, forest depressions, streams, savannahs, grasslands, borrow pits, lake margins, and rice paddies. Several authors have reported considerable variation in E. acutangula (Svenson 1929 [as E. fistulosa], 1939; Haines & Lye 1983; Browning et al. 1997). Svenson (1929, 1939) indicated E. planiculmis Steud. and E. fistulosa Schult. var. robusta Boeck. were potential segregates of E. fistulosa, which is treated herein as a synonym of E. acutangula. Hess (1953) described Heleochcharis pseudoistulosa H. Hess based on plants he collected in Angola, and stated that they differed from E. fistulosa in surface characteristics of the achene. Hess (1957) later provisionally
reported *H. cf. pseudofistulosa* from South America (Brazil), which differed in having terete rather than sharply three-angled culms; this is presumably *E. obtusetrigona* (Lindl. & Nees) Steud.

Svenson (1939) included *Eleocharis fistulosa* among five poorly defined tropical African taxa, and Browning et al. (1997) described variability among specimens of *E. acutangula* from different geographical areas in southern Africa. Our research reported here, including observations of live plants in the field and a study of herbarium specimens from a broad geographical area, shows considerable variability within *E. acutangula*, thus confirming the work of Svenson (1939) and Browning et al. (1997). A critical examination of over 600 specimens of *E. acutangula* suggested sufficient variation existed to warrant recognition of three infraspecific taxa: *E. acutangula* subsp. *acutangula*, *E. acutangula* subsp. *breviseta*, and *E. acutangula* subsp. *neotropica*. The objectives of this research were: (1) to investigate the morphological variation within *E. acutangula* and (2) to review all the apposite nomenclature in order to typify *E. acutangula* and its synonyms.

**METHODS**

Specimens were borrowed from herbaria that could provide loans yielding broad geographical representation of *Eleocharis acutangula* including types and authentic specimens. Over 600 specimens were examined from the following herbaria (acronyms follow Holmgren et al. 1990): BM, BRI, BRIT, C, CIIDIR, CM, E, F, FTG, GA, GH, IBE, ICN, K, LL, M, MEXU, MICH, MO, NH, NU, NY, P, PH, PRE, RSA, TAES, TEX, US, USF, VSC, WIS, Z, and ZT. Selected for multivariate analysis were 198 mature herbarium specimens (including types) complete for all morphological characters measured. Specimens studied originated from Africa, Australia, Bolivia, Brazil, China, Colombia, Cuba, Dominican Republic, Ecuador, El Salvador, Guyana, India, Japan, Madagascar, Malaysia, Mexico, Panama, Peru, United States, Venezuela, and Vietnam. Because of the limited number of specimens complete for all morphological characters, duplicate specimens collected by the same collector were measured. A complete citation of all specimens examined during this research can be found in Rosen (2006).

Quantitative and qualitative vegetative characters (e.g., culm height, width, texture, and cross-sectional shape; leaf sheath texture and structure; rhizome length and diameter) are highly plastic. Although these features are of some use in *Eleocharis* at the infrageneric level, they are of no value in distinguishing infraspecific taxa. In *Eleocharis* subg. *Limnochloa*, significant variation in culm anatomy in response to environmental conditions has been reported (Edwards et al. 2003; Baksh and Richards 2006). Svenson (1929) emphasized achene characters and perianth bristle texture in differentiating species of *Eleocharis*. A review of the literature reveals a tendency of workers investigating closely related species and infraspecific variation in *Eleocharis* to rely primarily on characters associated with the achene (Hines 1975; Larson & Catling 1996; Gregor 2003). Indeed, achene-related characters are important in taxonomic limits in *Eleocharis* at all levels (Menapace 1991).

Twenty morphological characters were selected for initial evaluation (Table 1). For each specimen a mature achene and its subtending scale were selected from near the base of a spikelet. Each specimen measured was complete for all characters so that the data matrix contained no missing values. One measurement per character was taken from each specimen, and 198 specimens (114 of *Eleocharis acutangula* subsp. *acutangula*, 67 of *E. acutangula* subsp. *breviseta*, and 17 of *E. acutangula* subsp. *neotropica*) were analyzed utilizing principal component analysis (PCA). The raw morphometric data were standardized and analyzed using NTSYSpc 2.11Q, and the principal components were generated using a correlation matrix (Rohlf 2000). A final analysis comprising six characters (Table 2) was run, and a scatter plot of the first two principal components was generated in an effort to depict morphological relationships.

**RESULTS**

The first three principal components represented 87.3% of the total variance (50.3%, 24.3%, and 12.7% for PC1, PC2, and PC3 respectively; Table 2) of 198 specimens scored for six morphological characters. Principal component 1 is most influenced by high positive loadings of LONBRSTL, TBRC1, BRSTLNACHNL
Table 1. Initial 20 morphological characters used to evaluate the infraspecific variation within *Eleocharis acutangula*.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Character</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACHNL</td>
<td>achene length (from base to constriction at neck)</td>
</tr>
<tr>
<td>ACHNLW</td>
<td>ratio of achene length to width (achene shape)</td>
</tr>
<tr>
<td>ACHNMAX</td>
<td>ratio of achene length to distance from achene base to widest point</td>
</tr>
<tr>
<td>ACHNNSCAL</td>
<td>(determines if achene is widest above, at, or below middle)</td>
</tr>
<tr>
<td>ACHNW</td>
<td>achene width (at widest point)</td>
</tr>
<tr>
<td>BRSTACH</td>
<td>number of perianth bristles longer than summit of achene</td>
</tr>
<tr>
<td>BRSTLACHN</td>
<td>ratio of length of longest perianth bristle to achene length</td>
</tr>
<tr>
<td>BRSTLACHNL</td>
<td>ratio of number of perianth bristles longer than summit of achene to total</td>
</tr>
<tr>
<td></td>
<td>number of perianth bristles</td>
</tr>
<tr>
<td>BRSTN</td>
<td>number of perianth bristles</td>
</tr>
<tr>
<td>LONBRSTL</td>
<td>length of longest perianth bristle</td>
</tr>
<tr>
<td>LONROW</td>
<td>number of longitudinal rows of cells on achene face</td>
</tr>
<tr>
<td>NECKWACHNW</td>
<td>ratio of achene neck width to achene width</td>
</tr>
<tr>
<td>NECKW</td>
<td>achene neck width</td>
</tr>
<tr>
<td>SCALEL</td>
<td>floral scale length</td>
</tr>
<tr>
<td>SCALELW</td>
<td>ratio of floral scale length to width</td>
</tr>
<tr>
<td>SCALEW</td>
<td>floral scale width</td>
</tr>
<tr>
<td>TBRACHW</td>
<td>ratio of tubercle width to achene width</td>
</tr>
<tr>
<td>TBRCCL</td>
<td>tubercle length</td>
</tr>
<tr>
<td>TBRCCLW</td>
<td>ratio of tubercle length to width (tubercle outline shape)</td>
</tr>
<tr>
<td>TBRCW</td>
<td>tubercle width</td>
</tr>
</tbody>
</table>

(Continued...)

Principal component 2 is most influenced by a high positive loading of NECKWACHNW and a high negative loading of TBRCIW (Table 2). Although there are varying degrees of overlap among the three taxa, specimens from each subspecies cluster together into distinct groups (Fig. 1). Specimens of *Eleocharis acutangula* subsp. *breviseta* and *E. acutangula* subsp. *neotropica* are almost completely separated along principal component axes 1 and 2 (Fig. 1). Specimens of *E. acutangula* subsp. *acutangula* overlap slightly with *E. acutangula* subsp. *breviseta* along principal component axis 1 and *E. acutangula* subsp. *neotropica* along principal component axis 2. The relatively small area of the graph (Fig. 1) occupied by *E. acutangula* subsp. *breviseta* and *E. acutangula* subsp. *neotropica* compared to that occupied by *E. acutangula* subsp. *acutangula* is presumably the result...
Table 2. Eigenvalues and total percent variance represented by each principle component and loadings onto the first three principle component axes for 6 morphological characters used in PCA of 198 specimens of *Eleocharis acutangula* subsp. *acutangula*, *E. acutangula* subsp. *breviseta*, and *E. acutangula* subsp. *neotropica*.

<table>
<thead>
<tr>
<th>Character</th>
<th>PC 1</th>
<th>PC 2</th>
<th>PC 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalue</td>
<td>3.018</td>
<td>1.459</td>
<td>0.760</td>
</tr>
<tr>
<td>Percent variance</td>
<td>50.302</td>
<td>24.317</td>
<td>12.675</td>
</tr>
<tr>
<td>LONBRSTL</td>
<td>0.862</td>
<td>0.365</td>
<td>0.030</td>
</tr>
<tr>
<td>TBRCL</td>
<td>0.832</td>
<td>-0.348</td>
<td>-0.290</td>
</tr>
<tr>
<td>BRSTLNACHNL</td>
<td>0.828</td>
<td>0.324</td>
<td>0.040</td>
</tr>
<tr>
<td>TBRCW</td>
<td>0.695</td>
<td>-0.643</td>
<td>-0.259</td>
</tr>
<tr>
<td>ACHNL</td>
<td>0.644</td>
<td>0.220</td>
<td>0.576</td>
</tr>
<tr>
<td>NECKWACHNW</td>
<td>0.015</td>
<td>0.799</td>
<td>-0.524</td>
</tr>
</tbody>
</table>

Table 3. Select character comparisons for *Eleocharis acutangula* subsp. *acutangula*, *E. acutangula* subsp. *breviseta*, and *E. acutangula* subsp. *neotropica*. Means and ranges (mean ± 1 standard deviation) are provided for quantitative characters.

<table>
<thead>
<tr>
<th>Character</th>
<th>subsp. <em>acutangula</em></th>
<th>subsp. <em>breviseta</em></th>
<th>subsp. <em>neotropica</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>achene length (mm)</td>
<td>1.8(1.6–2)</td>
<td>1.6(1.4–1.7)</td>
<td>1.7(1.6–1.8)</td>
</tr>
<tr>
<td>achene width (mm)</td>
<td>1.4(1.2–1.6)</td>
<td>1.3(1.2–1.4)</td>
<td>1.4(1.3–1.5)</td>
</tr>
<tr>
<td>achene color at maturity</td>
<td>shiny dark amber</td>
<td>shiny dark brown</td>
<td>shiny yellow-green (tinged with amber)</td>
</tr>
<tr>
<td>tubercle width (mm)</td>
<td>0.7(0.6–0.9)</td>
<td>0.7(0.6–0.8)</td>
<td>0.9(0.8–1)</td>
</tr>
<tr>
<td>achene neck width (mm)</td>
<td>0.6(0.4–0.7)</td>
<td>0.5(0.4–0.6)</td>
<td>0.8(0.7–0.8)</td>
</tr>
<tr>
<td>tubercle length (mm)</td>
<td>0.6(0.5–0.8)</td>
<td>0.4(0.3–0.5)</td>
<td>0.5(0.4–0.5)</td>
</tr>
<tr>
<td>ratio of achene neck width to achene width</td>
<td>0.4(0.3–0.5)</td>
<td>0.4(0.3–0.4)</td>
<td>0.5(0.6–0.7)</td>
</tr>
<tr>
<td>description of perianth bristles</td>
<td>usually all overtopping summit of achene and sometimes the tubercle; coarsely retrorse nearly to the base or less often completely smooth</td>
<td>usually few-none overtopping summit of achene; only a few short, salient retrorse spinules near the tips</td>
<td>all overtopping tubercle; coarsely retrorse nearly to the base</td>
</tr>
<tr>
<td>length of longest perianth bristle (mm)</td>
<td>2.6(2–3.3)</td>
<td>1.2(1–1.5)</td>
<td>3.6(3.2–4)</td>
</tr>
<tr>
<td>ratio of length of longest perianth bristle to achene length</td>
<td>1.4(1.1–1.7)</td>
<td>0.8(0.6–0.9)</td>
<td>2(1.9–2.3)</td>
</tr>
<tr>
<td>ratio of tubercle length to width</td>
<td>0.8(0.6–1.1)</td>
<td>0.6(0.5–0.8)</td>
<td>0.5(0.4–0.6)</td>
</tr>
</tbody>
</table>

of less morphological variability in *E. acutangula* subsp. *breviseta* and *E. subsp. neotropica*, which perhaps stems from their relatively limited geographical distributions when compared with the more morphologically variable and widespread *E. acutangula* subsp. *acutangula*. This could also indicate active speciation (local adaptation) in *E. acutangula* subsp. *acutangula*.

**Discussion and Conclusion**

Multivariate analysis and thorough examination of ca. 600 specimens, including types, warrants the recognition of three infraspecific taxa within *Eleocharis acutangula*. The presence of several conspicuous morphological differences between the three taxa along with a relatively cohesive geographic distribution of *E. acutangula* subsp. *breviseta* and *E. subsp. neotropica* (Fig. 2) suggests subspecies is an appropriate rank for classification (Stuessy 1990). A summary of the characters accounting for most of the variability in the multivariate analysis and our observations of achene color and the length and texture of perianth bristle
spines indicate that features of the mature achene and perianth are essential for identification of the subspecies of *E. acutangula* (Table 3). *Eleocharis acutangula* subsp. *breviseta* is distinguished from *E. acutangula* subsp. *acutangula* by its shorter achenes and tubercles and short perianth bristles with only a few short, retrorse spines near the tips. *Eleocharis acutangula* subsp. *neotropa* differs from *E. acutangula* subsp. *acutangula* by its long, soft, flexuous perianth bristles, weakly constricted achene apex, and the tubercle being usually as wide to wider than long. Differences between *E. acutangula* subsp. *breviseta* and *E. acutangula* subsp. *neotropa* are summarized in Table 3. Greater variability was observed in specimens referable to *Eleocharis acutangula* subsp. *acutangula* for several of the parameters used in the multivariate analysis (Fig. 1; Table 3). Variation was also observed in achene epidermal cell shape, often in achenes from the same herbarium specimen (Rosen 2006).

Svenson (1929, 1939) suggested that *E. fistulosa* var. *robusta* and *E. planiculmis* may represent taxa distinct from *E. acutangula*. However, a critical examination of the types indicates they are only minor expressions of highly variable *E. acutangula* subsp. *acutangula*. Specimens from Madagascar [DuPuy 2429 (MO, K, P); Bathie 17929 (P, US); and Bathie 2722 (P)], including type material of *E. fistulosa*, exhibited obtusely trigonous culms rather than sharply wing-angled triquetrous culms observed in all other specimens of *E. acutangula* examined. Indeed, the protologue of *S. fistulosus* describes the culms as “subtriquetro”. These specimens are otherwise referable to *E. acutangula* subsp. *acutangula* for the characters used in the multivariate analysis. We do not propose segregation on the basis of a single, highly plastic vegetative character and with such a limited number of specimens examined.

**TAXONOMIC TREATMENT**

### KEY TO SUBSPECIES OF *ELEOCHARIS ACUTANGULA*

1. Longest perianth bristle 3.2–4 mm long, soft, flexuous, retrorsely spinulose to below the middle (nearly to the base); achene neck weakly constricted, 0.6–0.7 times achene width; tubercle 0.4–0.6 times long as wide; mature achenes yellow-green (tinged with amber); distribution limited to northwest South America

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Plants perennial. Roots coarse, fibrous, drab-brown to reddish, small storage structures present in carefully collected plants, cylindrical-reniform, brown; primary rhizomes caudex-like, thick, hard, ascending, concealed by roots and persistent culm bases (occurring only in carefully collected specimens); secondary rhizomes elongated, to 4 mm thick, scales to 17 mm long (few seen). Culms triquetrous (a few specimens from Madagascar trigonous) distally, (25–)38–81(–135) cm long × (1.2–)2.1–4.4(–6.5) mm wide, soft, internally spongy, with incomplete transverse septa, smooth, green, finely longitudinally striate when dry. Leaves 2, reduced to sheaths, apically oblique, membranous, loose, friable, proximally pinkish to dark maroon (dark purplish), distally drab, apex acute. Spikelets cylindric, (11–)21–39(–56) mm long × (2.5–)3.2–4.8(–6) mm wide, acute; proximal scale with flower, obtuse, amplexicaul-clasping, appearing as a continuation of culm, remaining floral scales conspicuously spirally arranged, appressed to somewhat spreading at maturity, ovate-oblong, (2.5–)3.8–5.3(–6) mm long × (1.7–)2.3–3.4(–4.8) mm wide, cartilaginous, abaxially greenish to stramineous centrally, stramineous marginally, sparsely red-maculate and sometimes the veins or other areas reddish or pinkish (purplish) tinged, usually with a fine dark band near apex, adaxially sparsely to copiously red-maculate, apex acute (rounded), usually 1.1–1.8 times the length of the achene (rarely one or few just reaching its summit or slightly shorter), retrorsely spinulose nearly to base or rarely completely smooth (both conditions can occur in same population), stramineous or pinkish to dark maroon; stamens 3; anthers (1.1–)1.3–2.2(–3.2) mm long, stramineous; style 3-fid. Achenes biconvex, very broadly obovoid to obovoid, the shoulders and sides near the apex usually straight and forming an obtuse angle, or sometimes rounded, (1.4–)1.6–2.0(–2.2) mm long × (1.0–)1.3–1.6(–1.8) mm wide, with (11–)12–15(–19) longitudinal rows of deeply concave transversely oblong to linear polygonal cells visible through transparent periclinal layer on each achene face, dull yellow-buff maturing to shiny dark amber (dark brown), apex constricted to a distinct neck about 0.3–0.5 times the width of achene. Tubercle dorsoventrally compressed, shallowly triangular-deltate (triangular), 0.5–0.8(–1.1) mm long × (0.5–)0.6–0.9(–1.2) mm wide, stramineous, maturing to dark brown.

Fig. 2. Distribution of Eleocharis acutangula subsp. acutangula (open circles), E. acutangula subsp. breviseta (closed circles), and E. acutangula subsp. neotropica (triangles). Each symbol represents one or more specimens.
Lectotypification of *Eleocharis acutangula*

*Eleocharis acutangula* was described by Roxburgh (1820) as *Scirpus acutangulus* based on plants from India. As is the case with apparently all Roxburgh names, no type specimen was designated (Forman 1997). Schultes transferred *S. acutangulus* to *Eleocharis* without indicating a type. A literature search revealed no reference to a particular type specimen although a number of authors indicate the “type” is from India (e.g., Haines & Lye 1983; Gordon-Gray 1995; Browning et al. 1997). Typifying Roxburgh names can be difficult since his specimens were widely distributed, making locating specimens annotated by him or known to be associated with him challenging (Forman 1997). Almost all of Roxburgh’s nearly 2600 species were illustrated by color drawings prepared by local Indian artists; the original set is at CAL, and a duplicate set at K (Sanjappa et al. 1991). Forman (1997) indicated that the *Flora Indica* drawings were often superior to the corresponding Roxburgh specimen (if one can be found), and in some instances make a better choice for a type. From the set of drawings at Kew a high resolution digital photograph was obtained of the front and back of the drawing of *S. acutangulus*. The drawing, a stylized depiction of an immature plant, was annotated in what the first author interprets as Roxburgh’s hand.

We made queries to curators at key herbaria indicated by Forman (1997) in an effort to locate an authentic Roxburgh specimen. Mark Spencer (BM) presented a specimen (BM-000847992) that he considers to have been associated with Roxburgh, the most compelling evidence being annotations on the verso and front of the specimen. The verso is annotated “Ind. Orient Roxburgh” in an unknown hand, indicating that the specimen was received from Roxburgh, and the front was annotated “72” in what the first author interprets to be Roxburgh’s hand. We selected this specimen as the lectotype of *Scirpus acutangulus* since it fits the description in the protologue and is thought with reasonable certainty to have been used by Roxburgh.

Problems with Typification of *Scirpus medius*

Roxburgh described *Scirpus medius* as being similar to *S. acutangulus* but having shorter culms with smooth, rounded angles. Nees (1842) transferred the name to the genus *Limnochloa*. Roxburgh’s description of the culms as having rounded angles is troublesome, as all Asian specimens of *Eleocharis acutangula* examined during this research had triquetrous culms. No specimens annotated as *S. medius* were seen by us, and no specimens were located in herbaria where Roxburgh’s specimens were distributed. Thus, we follow Svensson (1929) and others (Blake 1939; Koyama 1985; Gordon-Gray 1995) in placing *S. medius* in synonymy under *E. acutangula*.

Clarification of the Authorship of *Eleocharis fistulosa*

*Scirpus fistulosus* Poir. is illegitimate because of an earlier homonym, *S. fistulosus* Forsskal. *Eleocharis fistulosa* Link is also invalid because Link failed to associate the specific epithet with the name of the genus or species, or with its abbreviation, as mandated by the Art. 33.1 of the ICBN (McNeill et al. 2006). Thus, *E. fistulosa* Schult. is the correct author citation (See ICBN Articles 58.1; 7.5; and 33, Note 2.). Since the priority of *E. fistulosa* does not date back to the publication of Poiret’s illegitimate use, *E. acutangula* (Roxb.) Schult. has priority as the oldest legitimate name for the species.

Lectotypification of *Eleocharis fistulosa* var. *robusta*

*Eleocharis fistulosa* var. *robusta* was described by Boeckeler based on *Schweinfurth 2326* from Central Africa. Boeckeler’s types were at B, and, if the holotype of *E. fistulosa* var. *robusta* was ever extant at B, it was destroyed by the fire of 1943 (Robert Vogt, B. pers. comm.). In this case, *Schweinfurth 2326* from GH is designated as lectotype, and two duplicates from Z become islectotypes.

Excluded Name

*Eleocharis fistulosa* var. *micrantha* Chermezon was described from specimens from Senegal (Chermezon 1936). Attempts to locate type specimens cited in the protologue have been unsuccessful thus far. Svensson (1939) relegated this name to synonymy under *E. nupeensis* Hutchinson & Dalziel based on the description, a temporary solution adopted here.


Distribution.—Panropical; in Mexico from the states of Chiapas, Hidalgo, Jalisco, Nayarit, Tabasco, and Veracruz-Llave. In Central America known from Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, and Panama. In the Caribbean basin known from Dominica, Dominican Republic, Grenada, and Jamaica. In South America known from records in Argentina, Brazil, Colombia, Ecuador, Guyana, Paraguay, Surinam, and Venezuela. Some previous reports of Eleocharis acutangula from the Galápagos Archipelago are based on misidentified specimens of E. obtusetrigona (Stewart 1911). Other reports were not verified (e.g., Jorgensen & Leon-Váñez 1999), and no authentic specimens of E. acutangula from the Galápagos Archipelago have been seen. Perhaps most widespread and occurring in more variety of habitats in tropical Africa, with records from Angola, Botswana, Burkiina Faso, Burundi, Cameroon, Central African Republic, Comoro Islands, Congo, Ethiopia, Gabon, Ghana, Guinea-Bissau, Ivory Coast, Liberia, Madagascar, Malawi, Nigeria,
Rhodesia, Senegal, Sierra Leone, South Africa, Sudan, Swaziland, Tanzania, Zaire, Zambia, and Zimbabwe. Of sporadic distribution in Asia and Oceania with records from Australia, China, India, Indonesia, Japan, Malaysia, Papua-New Guinea, Philippine Islands, Siam, Sri Lanka, and Vietnam.

Habitat.—Various disturbed and natural freshwater herbaceous and forested wetlands including marshy open grasslands, coastal savannas, and tropical forests from sea level to 2300 m. Reportedly forms expansive stands on a variety of soil types usually associated with other aquatic plants. Weedy in rice and other crop rotations and aquatic habitats, and used as a fiber crop in Borneo, Brazil, and Sumatra (Simpson & Inglis 2001).

Note.—Eleocharis acutangula subsp. acutangula as treated here remains a variable taxon and includes forms meriting additional systematic study. Of particular interest are plants reviewed from Madagascar (including the type of *E. fistulosa*) with obstruously trigonous culms.

2. **Eleocharis acutangula** (Roxb.) Schult. subsp. **breviseta** D.J. Rosen, subsp. nov. (Fig. 3 c–h). Type: DOMINICAN REPUBLIC. El Seibo Province, 3–7 Nov 1946, Howard & Howard 9862 (holotype: GH!, isotype: NY–2 sheets!, PI, US!).

*A Eleocharis acutangula* (Roxb.) Schult. subsp. *acutangula* perianthii setis brevioribus cum spinulis paucis retrorsis prope apicem, acheniis–

Plants perennial. Roots coarse, fibrous, mostly maroon (a few drab-brown), small storage structures present in carefully collected plants, cylindrical-reiform, white; primary rhizomes caudex-like, thick, hard, ascending, concealed by roots and persistent culm bases (occurring only in carefully collected specimens); secondary rhizomes elongated, to 3 mm thick, scales to 9 mm long (few seen). Culms triquetrous, (19–)30–71(–134) cm long × (1.1–)1.3–3.7(–7) mm wide, soft, internally spongy, with incomplete transverse septa, smooth, green when fresh, finely longitudinally striate when dry. Leaves 2, reduced to sheaths, apically oblique, membranous, loose, friable (upper distal portion disintegrating when submerged), proximally dark maroon, distally drab, apex acute. Spikelets cylindric, (10–)17–34(–49) mm long × (2.2–)2.7–4.1(–5.5) mm wide, acute; proximal scale with flower, obtuse, amplexicaul-clasping, appearing as a continuation of culm; remaining floral scales conspicuously spirally arranged, appressed to somewhat spreading at maturity, ovate-oblong, (3.1–)3.3–4.5(–5.9) mm long × (1.4–)1.8–3(–4.0) mm wide, cartilaginous, abaxially greenish centrally, stramineous marginally and sometimes reddish or pinkish tinged, with a fine dark band near apex, adaxially sparsely to copiously red-maculate, apex acute (rounded), distal 0.1–0.4 mm translucent hyaline-erosive, central area nearly flat, coarsely many veined, only mid-vein conspicuous in adaxial view. Flowers with (5–)6–7(–8) perianth bristles, bristles sub-equal, (0.4–)0.6–1(–1.2) times the length of achene (rarely few-all bristles overtopping achene summit) with only a few short, salient retrorse spinules near tips (rarely spinules present in distal half), stramineous or pinkish to dark maroon; stamens 3; anthers (0.9–)1.1–1.9(–2.7) mm long, stramineous; style 3-fid. Achenes biconvex, broadly obovoid, the shoulders and sides near the apex usually straight and forming an obtuse angle, (1.3–)1.4–1.8(–2.1) mm long × (1.1–)1.2–1.4(–1.6) mm wide, with (9–)11–14(–16) longitudinal rows of deeply concave transversely oblong (linear) polygonal cells visible through transparent periclinal layer on each achene face, dull yellow-green maturing through amber to shiny dark brown, apex constricted to a distinct neck about 0.4 times width of achene, in the field achenes sometimes persistent after the floral scales have shed giving spikelet a beaded appearance. Tubercle dorsoventrally compressed, shallowly triangular, (0.2–)0.3–0.5(–0.6) mm long × (0.5–)0.6–0.8(–1) mm wide, light brown tinged with green, maturing to dark brown.


MEXICO: Campeche: a approx. 10 km al sureste de la ciudad de Campeche, Mum. Campeche, alt. 80 m, 10 Nov 1980, Novelo & Zetina 721 (TEX), 14 km N of Ocozocautla on road to Mal Paso, Municipio of Ocozocautla de Espinosa, 07 Oct 1974, Breedlove 38254 (MEXU, MO).

Chiapas: 96 km S of Mexican Hwy. 190 on road to Nuevo Concordia, 10 Oct 1974, Breedlove 38516 (NY). Guerrero: 1.5 km al NW del Rincon de la Vía, 28 Sep 1988, Verduzo 389 (MEXU).

CENTRAL AMERICA. PANAMA: vicinity of El Llano, 7–8 Sep 1962, Duke 5526 (MO, USF), Near the big swamp east of the Rio Tecumene Province, 11 Dec 1923, Standley 26509 (MO).

Canal Zone: Laguna de Portala, near Chepo, province of Panama, Oct 1911, Pittier 4602 (NY). Panama: Sabanas near Chepo, 30 m, 20 Jan 1935, Hunter & Allen 87 (MO), 1.6 km W of Juan Diaz, 10 Oct 1917, Killip 4090 (PH, RSA, US), Camino del Boticario, near Chepo, altitude 30 to 50 meters, Oct 1911,
**Pittier 4557 (GH, NY, US)**, near Matias Hernandez, wet field, 30 Dec 1923, **Standley 28890 (US)**, near Matias Hernandez, wet field, 30 Dec 1923, **Standley 28894 (US)**. **CARIBBEAN BASIN. CUBA: Ciudad de La Habana:** Vedado-Habana, Habana de Monasterio, 23 Jun 1920, **Leon 9215 (NY)**. Without location, 1860–1864, **Wright 3376 (NY)**, mixed with E. mutata, MO, NY, P. **SOUTH AMERICA. COLOMBIA:** **Magdalena:** Rincon Honda, Magdalena Valley, 10 Aug 1924, **Allen 357 (MO)**. **Vaupes:** Rio Vaupes, Mitu y alrededores, 08 Sep 1951, **Schultes & Cabrera 11267 (GH)**, Rio Vaupes, Mitu and vicinity, 09 May 1953, **Schultes & Cabrera 12925 (GH)**–2 sheets. **VENEZUELA:** **Bolivar:** 27 km SW of Cacarica along Hwy. 19 to Ciudad Bolivar, 22 Nov 1973, **Davidse 4355 (MO)**. **Tachira:** between La Rochela and La Espuma, SW of Santo Domingo. 31 Jul 1979, **Steyermark & Lieder 189299 (MO)**. **Zulia:** Perija, carretera Calle Larga-San Felippe-Jaguacita, km 25 al SE de San Felipe, 09 Oct 1977, **Bunting 5656 (NY)**, ca 50 km SSW of Machiques by air, 19 km W of main road, 26 Mar 1982, **Liesner & Gonzalez 13183 (NY)**. **UYUGA:** **Takan-Takutu-Upper Essequibo Region:** Baboon Hill (Sarbina Taut) 1 5 km of Sand Creek Village, 21 Jun 1989, **Gillespie et al. 1803 (NY)**. **ECUADOR:** **Los Ríos:** along road San Juan, Vince, 07 Mar 1988, **Laegaard & Remotze 70632 (K, NY)**. **BAZIL:** **Mato Grosso do Sul:** Pantanal do Miranda-Abobral, Passo do Lontra, Rodovia MS 122, Fazenda Sao Bento, depois da 2ª porteira, 11 Jul 1997, **Rodrigues et al. 3 (K)**. **Rondonia:** Guapure, Porto Velho, 1952, **Cordeiro & Silva 270 (US)**. **Amapa:** Rio Macacoari, Municipio de Macapa, 05 Aug 1951, **Froes & Black 27231 (US)**. **Parana:** Curitiba, Paso do Lontra (mun. Miranda) Mato Grosso, 13 Oct 1972, **Hatschbach & Scherer 30441 (NY, Z)**. **Rio de Janeiro:** Rio de Janeiro, Jan 1914, **Hoehne 5736 (US)**. **Rio Grande do Sul:** Jari, estrada do Caracuru, Jari, estrada do Caracuru, campo alagado, 09 Aug 1869, **Silva 2636 (NY)**. **Roraima:** borrow pit close to road from Furo do Maraca to SEMA research station, 10 Mar 1987, **Edwards 2529 (K)**. **BOLIVIA:** **Beni:** Ballivian, la zona de influencia del rio Yacuma, 09 Mar 1980, **Beck 3248 (NY)**, Ballivian, espiritu en la zona de influencia del rio Yacuma, 13 Apr 1980, **Beck 3354 (NY)**. **AFRICA. SOUTH AFRICA:** **KwaZulu-Natal:** Hlabsa, St. Lucia, E shores, 30 Nov 1959, **Froel & Ward 15 (K, M, NY–2 sheets)**. Near Howick, 1990, **Taylor 131 (NU)**, Ingaviguama distr., near Salumhlanga, Ndumu Game Reserve, 24 Dec 1972, **Pooley 1624 (NU)**, Greater Durban area, Mlazi Valley, 15 Mar 1992, **Ward 11925 (NU, PRE)**, Greater Durban area, Mlazi Valley, 15 Mar 1992, **Ward 11926 (NU, NH photo)**, Transvaal, Waterberg, 12.3 m NW of Warmbaths, 19 Mar 1965, **Acocks 23562 (K, PRE)**, near Maputsa, Tengane near Nyinyani, 29 Oct 1980, **Cunningham s.n. (NU)**, Karkloof floodplain near junction with Kusane River, 17 Jan 1977, **Kotze s.n. (NU)**. **TANZANIA:** **Singida Dist.:** T. 5, M. 12.7 from Issuma on the Singida-Mayoni Road, 4800 ft, 13 Mar 1964, **Greenway & Pollard 11543 (PRE)**, T4, Humbwanga Dist., goh Mubikga, 5 km S of Humbwanga, 19 Jun 1996, **Faden et al. 96/302 (US)**, T5, Manyoni Dist., Chaya Lake, S of Itigi-Tabora track, 16 km W of Kazikazi, 02 Jul 1996, **Faden et al. 96/522 (US)**. **ZIMBABWE:** Gwelo, Sengwa Nature Reserve, Jan 1966, **Jacobsen 73 (NU)**, District Gwelo, Sengwa research station, 09 May 1966, **Jacobsen 3218 (PRE)**.

**Distribution.**—In the U.S.A. known only from Lee County, Florida. In Mexico known from the states of Campeche, Chiapas, and Guerrero, and in Central America known only from Panama. In the Caribbean Basin known only from Cuba and the Dominican Republic. Most widespread in South America with records from Bolivia, Brazil, Colombia, Ecuador, Guyana, and Venezuela. In Africa known from South Africa, Tanzania, and Zimbabwe.

**Habitat.**—Disturbed and natural freshwater wetlands including marshy open grasslands and tropical forests; reported from 0–1400 m.

**Etymology.**—The subspecific epithet is indicative of the short perianth bristles of this taxon.

3. **Eleocharis acutangula** ( Roxb.) Schult. subsp. neotropica D. J. Rosen, subsp. nov. (Fig. 3 i–k). Tipe: PERU. **DEPARTAMENTO DE LOROEO: Maynas, Iquitos, prolongacion Yavari, Versailles-Patna, open annually burned grassland, 23 Mar 1974, McDaniel & Rimachi 18552 (K, MO!; isotypes: IBE–2 sheets [photos!], NY!).

A *Eleocharis acutangula* (Roxb.) Schult. subsp. *acutangula* perianthii setis breviribus mollibus flexuosis longissimis 1.8–2.4–plio longitudi achenii, achenii apicibus constrictis usque ad 0.6–0.7-plio latitudem achenii et stylopodis plurumque latioribus quam longioribus recedit.

**Plants** perennial. **Roots** coarse, fibrous, drab-brown; primary rhizomes caudex-like, thick, hard, ascending, concealed by roots and persistent culm bases; secondary rhizomes elongated, to 3.2 mm thick, scales to 14 mm (few seen). **Culms** triquetrous, (44–)56–86(–106) cm tall × (2–)2.7–3.9(–4.3) mm wide, soft, internally spongy, with incomplete transverse septa, smooth, green to drab gray-green and finely longitudinally striate when dry. **Leaves** 2, reduced to sheaths, apically oblique, membranous, loose, friable, proximally dark maroon, distally drab, apex acute. **Spikelets** cylindric, (1.5–)2–3.1(–3.5) cm long × (3–)3.2–4.2(–4.5) mm wide, acute; proximal scale with flower, obtuse, clasping, appearing as a continuation of culm; remaining floral scales conspicuously spirally arranged, appressed, ovate-widely ovate, (3.9–)4.1–4.8(–5) mm long × (2.3–)2.4–3.2(–3.8) mm wide, cartilaginous, stramineous (faintly greenish centrally), adaxially sparsely red-maculate, apex acute (rounded), the distal 0.2–0.3 mm translucent hyaline-erosive, central area nearly flat, abaxially coarsely many veined, the veins raised and visible at 20×, only mid-vein distinguishable in adaxial view. **Flowers** with (5–)6–7 perianth bristles, bristles sub-equal, (1.8–)1.9–2.3(–2.4) times achenie
length, coarsely retrorsely spinulose nearly to base, stramineous, sometimes becoming reddish-brown distally; stamens 3; anthers 0.9–1.8(–2.3) mm long, stramineous; style trifid. **Achenes** biconvex, broadly obovoid, (1.3–)1.6–1.8 mm long × (1.2–)1.3–1.5(–1.6) mm wide, with 12–14(–16) longitudinal rows of deeply concave transversely oblong polygonal cells visible through transparent periclinal layer on each achene face, dull to shiny yellow-green (sometimes tinged with amber), apex constricted to a distinct neck about 0.6–0.7 times achene width. **Tubercle** dorsoventrally compressed, wider than tall and appearing very shallowly to shallowly triangular, sometimes apex appearing truncate or retuse, (0.3–)0.4–0.5(–0.6) mm long × (0.6–)0.8–1(–1.1) mm wide, light-dark brown.


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