A SYSTEMATIC STUDY OF SELECT SPECIES COMPLEXES OF *ELEOCHARIS* SUBGENUS *LIMNOCHLOA* (CYPERACEAE)

A Dissertation

by

DAVID JONATHAN ROSEN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2006

Major Subject: Rangeland Ecology and Management

A SYSTEMATIC STUDY OF SELECT SPECIES COMPLEXES OF *ELEOCHARIS* SUBGENUS *LIMNOCHLOA* (CYPERACEAE)

A Dissertation

by

DAVID JONATHAN ROSEN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Approved by:

Chair of Committee,	Stephan L. Hatch
Committee Members,	J. Richard Carter
	William E. Fox III
	James R. Manhart
	Fred E. Smeins
Head of Department,	Steven G. Whisenant

December 2006

Major Subject: Rangeland Ecology and Management

ABSTRACT

A Systematic Study of Select Species Complexes of *Eleocharis* Subgenus
Limnochloa (Cyperaceae). (December 2006)
David Jonathan Rosen, B.S., Texas State University;
M.S., Texas A&M University
Chair of Advisory Committee: Dr. Stephan L. Hatch

A systematic study of two complexes of closely related species within *Eleocharis* subg. *Limnochloa* was conducted to better define poorly understood species and to lay the foundation for a worldwide revision of this group. Research utilized scanning electron microscopy (SEM), study of more than 2300 herbarium specimens and types from 35 herbaria, multivariate analysis, and field studies in the southeast United States and Mexico. Examination of achene gross- and micromorphology using SEM indicated a relationship among the species of the *Eleocharis mutata* complex (comprising *E*. *mutata*, *E*. *spiralis*, and *E*. *cellulosa*), their distinctness from the *E*. *acutangula* complex (comprising *E*. *acutangula* s.l. and *E*. *obtusetrigona*) and support the placement of all taxa studied within subg. *Limnochloa*. All species examined shared micromorphological characters typical of subg. *Limnochloa*. A systematic study of the worldwide morphological variation of *E*. *mutata* suggests it is represented by a single taxon throughout its distribution and is native to the New World and probably introduced in tropical Africa. The taxonomic relationship of *Eleocharis mutata* and *E*. *spiralis* was explored using discriminant analysis, PCA and phyto-geography, supporting the recognition of the two taxa as distinct at the rank of species. A systematic study of *E*. *cellulosa* suggests it is represented by a single taxon throughout its distribution, with an apparent Caribbean genotype distinguished by the presence of perianth bristles with retrorse spinules. A systematic study of the worldwide variation of *E*. *acutangula* s.l. resulted in its segregation into two infraspecific taxa, *E*. *acutangula* subsp. *acutangula* and *E*. *acutangula* subsp. *breviseta*, and two new South American species, *E*. *neotropica* and *E*. *steinbachii*. Nomenclatural history and lectotypification of certain taxa studied are discussed, and two basyionyms and two synonyms of accepted taxa are lectotypified. A taxonomic treatment is provided that includes a key, detailed descriptions and complete synonymy of each species, line drawings prepared from select specimens examined, and notes on habitat and distribution. Future research goals and needs are discussed.

DEDICATION

This dissertation is dedicated to my grandparents Max and Molly Freedman, my brother Sam Rosen, and my good friend Robert M. Combs. Your passing has left a void in my life that will never be filled.

ACKNOWLEDGMENTS

I would like to offer my sincere thanks to my major professor Dr. Stephan Hatch for providing me the opportunity to earn this degree when others would not, and for his wisdom, direction, encouragement, and patience. I thank my committee members, Dr. Bill Fox, Dr. Jim Manhart, and Dr. Fred Smeins for reviewing my research, and for challenging me to expand the depth and breadth of my knowledge. I offer special thanks to Dr. Richard Carter for agreeing to serve as a special appointment, for being a mentor and friend, for companionship during field work in Texas, Florida, and Mexico, and for critically reviewing this research with patience and enthusiasm. Special thanks are due to Dr. M. Socorro González-Elizondo for suggesting several research problems, for sharing her expertise, and for being a friend, mentor, and generous host during my field work in Mexico. Special thanks are also due to José Marcos Pinedo Reyes for his assistance in the field, and especially for driving us over 3800 km through central and southern Mexico. I'd like to acknowledge numerous colleagues near and far who provided assistance and freely shared their knowledge and offered advice: Stanley Jones, J. Wipff, Fran Menapace, Galen Smith, Tony Reznicek, Eric Roalson, Paul Peterson, Rob Naczi, Mark Strong, and Charles Bryson. I am grateful to Dale Kruse for requesting loans for my research, and the curatorial and library staff of all of the herbaria mentioned for loan of specimens for study, assistance with questions about the disposition of certain specimens, types, and literature, and assistance with nomenclatural questions. I am especially grateful to Mark Spencer, Vicki Noble, and Peter Stafford (BM), Hajo Esser (M), Ib Friis (C), Jill Marsden (K), Kanchi Gandhi (GH), and Gina Murrell (CGE) for their friendly responses to my endless queries. I am extremely grateful to my friend Neva Mikulicz for preparing the excellent illustrations, to Alain Touwaide for translating the Latin diagnoses, to Mike Pendleton at the Microscopy Imaging Center for assistance, to Susan Knock for use of her lab, and to Larry Brown for requesting loans and types for me to study at SBSC. Above all, I thank my wife Kimberly and daughter Molly. Like Papa used to say, I make the living, and you make life worth living! I gratefully acknowledge financial support for research related expenses, supplies and travel from the Frank W. Gould Award for Graduate Student Research in Plant Systematics, Springfield Research Award, McCord Scholarship, and Mills Scholarship.

TABLE OF CONTENTS

LIST OF FIGURES

FIGURE Page

FIGURE Page

LIST OF TABLES

CHAPTER I

INTRODUCTION

Cyperaceae Juss., the third largest family of monocotyledons, comprise approximately 5,000 species in about 104 genera (Goetghebeur 1987, 1998). Cyperaceae are well represented in temperate, sub-arctic, and especially tropical regions worldwide from sea-level to over 5000 m (absent from Antarctica). Typically one of the largest families in most floristic treatments, it is probably the seventh largest worldwide (Reznicek 1990). The family has several very large cosmopolitan genera including *Carex* L. (ca. 2,000 spp.) and *Cyperus* L. (ca. 600 spp.; Goetghebeur 1998). Cyperaceous genera are concentrated in northern South America, southern Sudano-Zambesian Africa, and SW Australia (Goetghebeur 1998). Endemism in the family, at the generic level, is also concentrated in tropical America, tropical South Africa, and Australia (Goetghebeur 1998).

Members of Cyperaceae are mostly anemogamous and autogamous, though insect pollination has been suggested for several taxa with brightly colored inflorescence bracts (*Rhynchospora* Vahl sect. *Dichromena* Michx.), penultimate leaves (*Ficinia* Schrad.), or anther filaments (*Chrysithrix* L.; Leppik

---

This dissertation follows the style and format of the journal Sida.

1955; Dahlgren et al. 1985). Insect pollination has also been suggested for *Rhynchospora* Vahl (Schultze-Motel 1967), and Goetghebeur (1998) cites examples of numerous other genera.

Most species occur in mesic to hydric habitats, though the family is represented in almost all terrestrial environments. In North America numerous sedges are restricted to dry, well-drained sites (e.g., *Bulbostylis capillaris* (L.) Kunth *ex* Clarke, *Carex tenax* Chapman *ex* Dewey, *Cyperus nashii* Britton *ex* Small, and *Cyperus grayi* Torr.). Numerous species have been observed to host mycorrhizal fungi (Muthukumar et al. 2004). Intergeneric hybrids are apparently rare but have been reported (Fernald 1918).

Cyperaceae are dwarf to robust annual and perennial herbs, although a few taxa form woody scandent stems (e.g., *Gahnia* J.R. Forst. & G. Forst.) or are dwarf shrub-like in habit as in *Microdracoides* Hua (Dahlgren et al. 1985). Generally, the following suite of salient characters facilitates recognition of Cyperaceae: trigonous to triquetrous solid (hollow) culms; tristichous phyllotaxy with closed leaf sheaths; extremely contracted inflorescences of various arrangements with flowers subtended by scales; perianth segments absent, or modified to bristles, hairs, or scales; basifixed anthers; and one-seeded indehiscent fruits (=achenes). Of almost universal occurance in Cyperaceae are paracytic stomata that are almost always more numerous on the adaxial leaf surface and cone-shaped silica bodies commonly present in epidermal cells associated with vascular bundles (Dahlgren et al. 1985). Both C_3 and C_4

photosynthetic pathways occur in the family (Goetghebeur 1998). A thorough, illustrated survey of the vegetative and reproductive morphology of Cyperaceae is provided by Haines & Lye (1983).

The basic inflorescence unit in Cyperaceae is a spikelet. Eiten (1976) described the cyperaceous spikelet as a racemosely branched structure consisting of an axis (rachilla) of potentially indefinite growth bearing lateral true flowers, each subtended by a floral scale. Indeed, the branching pattern or ultimate branching orders of the inflorescence are important characters used to divide the family into subfamilies, tribes, and sub-tribes (Holttum 1948; Eiten 1976). Most novice cyperologists must first familiarize themselves with myriad inflorescence and spikelet arrangements of the family in their flora before attempting the use of diagnostic keys, and before accurate identifications can be made. This task is complicated by the extremely contracted inflorescences and reduced floral parts. The family, though well defined, comprises many taxonomically challenging taxa.

Cyperaceae are thought to have evolved during the Tertiary Period, with fossil records traced to the Eocene (Raven and Axelrod 1974; Daghilian 1981), and have a West Gondwana origination (Bremer 2002). Goetghebeur (1998) reported that fossils of Cyperaceae are only known with certainty from Paleocene times. Cronquist (1981, 1988) placed Cyperaceae with Poaceae (R. Br.) Barnhart in Cyperales, a classification scheme previously of long standing. Metcalfe (1971) and Dahlgren and Rasmussen (1983), however, considered

Cyperaceae a close relative to Juncaceae Durande. Cronquist (1988) regarded any similarity between Cyperaceae and Juncaceae as evolutionary parallelism, yet provided few characters shared by Cyperaceae and Poaceae besides their reduced commelinid floral morphologies.

Grant (1971) and Plunkett et al. (1995) provide a host of cytological, embryological, and morphological features shared by Cyperaceae and Juncaceae which are otherwise uncommon in commelinid monocots including polycentric chromosomes (=diffuse centromeres), postreductional meiosis, agmatoploidy, tetradinous pollen, tristichous phyllotaxy, onagrad embryo development, 5-oxy-methyl-flavones, and anatropous ovules. Recently, insights from DNA sequence analysis place Cyperaceae in a clade near Juncaceae and, in fact, suggest Cyperaceae are derived from Juncaceae (Plunkett et al. 1995; Bremer 2002; Soltis et al. 2005). Indeed, Blaser's (1941) early extensive morphological and anatomical research of the inflorescences of Cyperaceae demonstrated their great dissimilarities with Poaceae. Menapace (1991a) provided a thorough discussion and literature review of comparisons of Cyperaceae to Juncaceae and Poaceae.

Cyperaceae are economically important worldwide, especially as food, animal forage, fiber, fuel, medicines, ornamentals, and weeds. The important contribution of Cyperaceae to soil fertility and stability in reducing soil losses to erosion is largely undocumented (Simpson & Inglis 2001). Simpson & Inglis (2001) provide a checklist of 45 genera and 502 species of Cyperaceae with economic, ethnobotanical, and horticultural importance. The following accounts are of Cyperaceae with more widely known economic importance. *Cyperus papyrus* L., was an important source of paper, building material, fiber, and medicines to ancient Egyptian culture, and reportedly continues to be cultivated for industrial paper production in Uganda and Sudan (Haines & Lye 1983). *Eleocharis dulcis* Trinius *ex* Hensch. (Chinese water-chestnut) is cultivated in China, Taiwan, and Thailand for its edible tubers (Osotsapar & Mercado 1976; Vaughan & Geissler 1997). Holm (1977) lists five species of Cyperaceae among the worlds worst weeds; *Cyperus difformis* L., *C*. *esculentus* L., *C*. *iria* L., *C*. *rotundus* L., and *Fimbristylis miliacea* (L.) Vahl. In North America, *Eleocharis* is gaining importance in aquatic habitat restoration and enhancement (Fraser & Kindscher 2001).

Cyperaceae was originally described by Jussieu (1789). Goetghebeur (1998) organized the family into four subfamilies and 14 tribes based on a combination of characters from flower, inflorescence, and embryo morphology. Goetghebeur’s (1998) scheme is as follows with subfamilies followed by their respective tribes parenthetically: 1. **Mapanioideae** (Hypolytreae, Chrysitricheae); 2. **Cyperoideae** (Scirpeae, Fuireneae, Eleocharideae, Abildgaardieae, Cypereae, Dulichieae, Schoeneae); 3. **Scleriodeae** (Cryptangieae, Trilepideae, Sclerieae, Bisboeckelereae, two monotypic genera *incertae sedis* including *Exochogyne* C.B. Clarke and *Koyamaea* W.W. Thomas & Davidse); and 4. **Caricoideae** (Cariceae).

Morphologically distinct and well demarcated in Cyperaceae is the genus *Eleocharis* R. Br., with an inflorescence reduced to a single terminal spikelet (thus, unispiculate), basal leaves reduced to two (three) tubular sheaths, and a persistent style base forming a tubercle. Morphological features previously unknown in *Eleocharis* or its sections were recently reported for the first time including branched dimorphic culms, functionally staminate aerial spikelets, isolated trigonous achenes mixed with biconvex ones in section *Eleogenus*, and basal, subterranean spikelets in section *Eleogenus* (Gonzalez-Elizondo & Reznicek 1996).

Eleocharis is a worldwide genus of about 200 species with about 600 published names with a concentration of taxa in tropical America (González-Elizando & Tena-Flores 2000). The structural simplicity of *Eleocharis* and paucity of phylogenetically informative characters make it one of the most taxonomically difficult genera in the Cyperaceae (González-Elizando & Tena-Flores 2000). Taxa in *Eleocharis* of hybrid origin have recently been reported (Catling and Hay 1993; Catling 1994). The name *Eleocharis* first appeared in Robert Brown's (1810) *Prodromus Florae Novae Hollandiae*. Brown (1810) set apart *Eleocharis* from *Scirpus* based principally on the presence of a unispiculate culm and persistent style base articulated with the achene. Difficulty has arisen in the application of this character in regards to series *Pauciflora* (Svenson 1929). It is conjectured that Brown created the name by combining two Greek nouns; ἕλοζ (heleios) meaning "a marsh" and χ**ά**ριζ (charis) meaning grace, presumably referring to the aquatic habitat and graceful form of the genus as he first encountered it (Svenson 1929).

Whether intentionally or by oversight, Brown did not include an initial letter “h”, represented in the Greek by a rough breathing sound (Svenson 1929). An orthographic conundrum followed, as some authors, without justification, inserted the “h” forming the name *Heleocharis* (e.g., Lestiboudois 1819; Barros 1928). Despite the etymological preference of *Heleocharis* over *Eleocharis*, the *International Code of Botanical Nomenclature* is clear (Article 73) in that there is no validity of the altered spelling, and *Eleocharis* must be conserved (Greuter et al. 2000). Clark (1908) rejected all combinations made under *Heleocharis*, an uncompromising approach that only complicated the nomenclatural dilemma. In modern times, the predicament has been resolved with most taxonomists opting to treat *Heleocharis* as a trivial alternate spelling; a nomenclaturally sound solution, and one long-utilized in *Index Kewensis* (Svenson 1929). This solution is followed herewith, and consequently, alternate combinations utilizing *Heleocharis* are not considered in discussions of synonymy of each species treated in this manuscript.

North American *Eleocharis* were first monographed by Torrey (1836), and later by Britton (1889). Several historic enumerations of *Eleocharis* worth mentioning here include Röemer & Schultes (1817), Kunth (1837), Steudel (1855), and Thwaites (1864). The lectotype for the genus, *E. palustris* (L.) Roem. & Schult., was designated by Britton (1907). The genus was treated comprehensively by Svenson (1929, 1934, 1937, 1939), representing the first attempt to critically compare Old World and New World species. Svenson's (1957) subsequent monograph of North American *Eleocharis* forms the basis of classification upon which most recent infrageneric studies are derived. The significant contributions of Svenson have been an important reference during all aspects of this research and taxonomic treatment. More current taxonomic research in *Eleocharis* has focused on regional floristics (e.g. Barros 1960; Hooper 1972; Kern 1974; Haines and Lye 1983; Koyama 1985; Wilson 1993; González-Elizondo 1994, 2002), new species descriptions and name combinations (e.g. Simpson 1987; González-Elizondo and Reznicek 1996; Roalson 1999; Smith 2001), and infrageneric revision (e.g. Strandhede 1966; Hines 1975; Kukkonen 1990; Menapace 1991a; González-Elizondo and Peterson 1997; Roalson and Friar 2000). A comprehensive literature search has revealed some morphometric numerical taxonomic investigations of closely related species belonging to several troublesome complexes (Hines 1975; Żukowski & Klimco 1979; Larson & Catling 1996; Gregor 2003).

Most authors place *Eleocharis* within the tribe *Scirpeae* Kunth *ex* Dumort. (Tucker 1987; Kukkonen 1990; Bruhl 1995). Goetghebeur (1986) erected the tribe *Eleocharideae* Goetghebeur comprising *Eleocharis* and the derived genera *Websteria* S. H. Wright and *Egleria* G. Eiten. An extensive taxonomic history of *Eleocharis* can be found in Kukkonen (1990) and González-Elizondo and Peterson (1997). However, a brief summary is offered here.

Most early authors treated species now in *Eleocharis* as *Scirpus* L., notably Gray (1821). Lestiboudois (1819) segregated species of *Eleocharis* with two style branches to the genera *Heleocharis* and *Heleophylax* P. Beauv. *ex* T. Lestib. [= *Schoenoplectus* (Rchb.) Palla], and three style branches to the genus *Limnochloa* P. Beauv. *ex* T. Lestib. Later, Lestiboudois (1827) classified species of *Eleocharis* in several unranked groups within *Scirpus*: *Isolepis*, *Heleocharis*, and *Limnochloa*. Additional *Eleocharis* species were placed in the genera *Megadenus* Raf., *Clavula* Dumort., and *Baeothryon* A. Dietr. (Lestiboudois 1827). Nees von Esenbeck (1834a, 1834b) segregated species among *Eleocharis* and *Limnochloa*, and three newly described genera, *Chaetocyperus* Nees, *Eleogenus* Ness, and *Scirpidium* Nees. Subsequently, three additional genera were described: *Chlorocharis* Rikli, *Heleonema* Suess., and *Chamaegyne* Suess. (Rikli 1895; Süssenguth 1943).

The infrageneric classification of *Eleocharis* has been tumultuous over the last two-hundred years, with numerous classifications proposed (e.g. Torrey 1836; Kunth 1837; Bentham & Hooker 1883; Clarke 1900,1902, 1908; Beauverd 1921; Svenson 1929, 1934, 1937, 1939; Zinserling 1959; Blake 1939; Koyama 1961; Egorova 1976, 1980, 1981; Egorova and Khoi 1980; Kukkonen 1990; González-Elizondo and Peterson 1997; Roalson and Friar 2000). Svenson's (1929) worldwide monograph included a conservative classification of eleven series and six subseries. More recently, Kukkonen (1990) and González-Elizondo and Peterson (1997) have proposed a more complex, morphologically based infrageneric classification comprising 4 subgenera, 7 sections, 8 series, and 7 subseries. Roalson and Friar (2000) recently published yet another classification scheme based on analysis of internal transcribed spacer regions of nuclear ribosomal DNA. Among the three infrageneric classification systems only one group, Subgenus *Limnochloa*, is congruent.

Eleocharis subg. *Limnochloa* (P. Beauv. *ex* Lestib.) Torr. has also been variously treated by authors as series *Mutatae* Svens. and genus *Limnochloa* P. Beauv. *ex* Lestib. Nees von Esenbeck is sometimes recognized as author of a later homonymic *Limnochloa*, but merely revised the description and circumscription of the genus, crediting the name to Palisot de Beauvois (González-Elizondo and Peterson 1997). In his worldwide treatment, Svenson (1929) treated 15 species under ser. *Mutatae*, and separated it from other series by a combination of coarse culms (often as thick as the spikelet), and un-keeled (obscurely keeled) indurate scales. González-Elizondo and Peterson (1997) reported 21 species for subg. *Limnochloa*. *Eleocharis* section *Limnochloa* (P. Beauv. *ex* Lestib.) Benth. & Hook. is further distinguished by large, biconvex (rarely trigonous) achenes sculptured with polygonal cells, and the often fertile lowest scale which appears to be a continuation of the culm (González-Elizondo and Peterson 1997). *Eleocharis* subg. *Limnochloa* includes several ecologically and economically important species. *Eleocharis mutata* (L.) Roem. & Schult. is important in Brazil where it rapidly colonizes coastal lagoons (Palma-Silva et al. 2000), and *E*. *dulcis* (Chinese water chestnut) is widely cultivated for its edible tubers (Osotsapar and Mercado 1976). Despite the usually large and conspicuous habit of this group, new species have been described recently, including *E. sundaica* Kern (Malaysia; Kern 1958), *E. lankana* T. Koyama (Sri Lanka; Koyama 1974), *E. eglerioides* S. González & Reznicek and *E. liesneri* S. González & Reznicek (Venezuela; S. González & Reznicek 1996), *E. yecorensis* E. H. Roalson (Mexico; Roalson 1999), *E. laeviglumis* Trevisan & Boldrini (Brazil; Trevisan & Boldrini 2006), and several provisional species from Northern Territory, Australia (Cowie et al. 2000).

No comprehensive study of subg. *Limnochloa* (from Latin *limn*-, pertaining to standing water, and Greek *chloe*, green grass) has been published since the seminal work of Svenson (1929-1939). Subg. *Limnochloa* is in need of a revision considering the time that has lapsed since Svenson's treatment and the number of new species described. A review of the literature also reveals that the taxonomic relationships within subg. *Limnochloa* have never been thoroughly and broadly investigated. Svenson (1929) pointed out the occurrence of triangular achenes in series *Mutatae* as only occurring in the slender culmed *Eleocharis elongata* Chapm., and occasional triangular achenes and slender culms in *E. robbinsii* Oakes and *E. plicarhachis* (Griseb.) Svenson. A taxonomic study of these segregates has never been published. Menapace (1991b) demonstrated the potential for achene micromorphology to aid in assigning sectional or serial rank within subg. *Limnochloa*. Kukkonen (1990) assigned *Eleocharis dulcis* to subg. *Limnochloa* sect. *Limnochloa*, and Browning et al. (1997) assigned five species to sect. *Limnochloa*, neither providing any phenetic basis for this classification, nor did they examine specimens from throughout the geographic range of the taxa treated. Indeed, further classification within subg. *Limnochloa* is necessary to elucidate the evolutionary relationships of its members and facilitate its much needed revision.

Incongruous accounts by previous workers suggest that the taxonomic relationships of some variable or closely related taxa are still in need on study. Several authors have commented on the complexity of *Eleocharis acutangula* (Roxb.) Schult., the most widely distributed member of the group (Svenson 1939), and having the most extensive synonymy and tumultuous nomenclatural history (e.g., Svenson 1957; Browning et al. 1997). Svenson (1939; 1957) placed *E*. *obtusetrigona* (Lindl. & Nees) Steud. in synonymy under *E*. *fistulosa* Schult. which is currently accepted as a synonym of *E*. *acutangula*, whereas others treated it as a variety of *E*. *mutata* (Clarke 1898) or *E*. *fistulosa* (Barros 1960). González-Elizondo et al. (2002) recently recognized *E*. *obtusetrigona* as a distinct species.

Clarke (1900) considered *Eleocharis mutata* and *E*. *spiralis* (Rottb.) Roem. & Schult. to be quite different, whereas Kern (1974) suggested that *E*. *spiralis* was very near, and might better be treated as a subspecies of *E*. *mutata*. Svenson (1929) suggested that *E*. *mutata*, *E*. *cellulosa* Torr., and *E*. *spiralis* formed a group of closely related species. Specimens of *E*. *cellulosa* with trigonous culms and toothed bristles have been reported from Mexico, and it has been suggested that the variation in this species throughout its range is in need of investigation (González-Elizondo, personal communication). No detailed phenetic study of these three taxa and their synonyms has been published. Svenson (1929) treated *E*. *austro-caledonica* Vieill. as a synonym of *E*. *dulcis*, and then later under *E*. *spiralis* without explanation (Svenson 1939).

Browning et al. (1997) commented on the occurrence of variants among sympatric populations of *Eleocharis acutangula* and *E*. *dulcis*, some of which might warrant the establishment of new taxa. Their conclusions that *E*. *mutata* is of hybrid origin derived from *E*. *acutangula* and *E*. *dulcis* is problematic. Roalson (1999) pointed out that *E*. *mutata* was described from the New World and only recently accounted for in Africa (Hooper 1972; Haines & Lye 1983; Browning et al. 1995).

The worldwide variation of *E*. *mutata* and *E*. *acutangula* has not been studied. Indeed, Roalson (1999) suggested population studies of *E*. *mutata* were necessary to understand better what is being called *E*. *mutata* in Africa. Klimko (1988) published a cursory systematic study of African specimens of *E*. *acutangula* and *E*. *variegata* (Poir.) C. Presl., two species considered here to be quite distinct. Infraspecific variation occurs in sedge species with cosmopolitan distribution and has been documented in widely distributed species such as *E*. *palustris* (L.) J. Roem. & Schult., and *E*. *mamillata* (H. Lindb.) H. Lindb. (Smith 2001; Gregor 2003). Population studies of *E*. *mutata* and *E*. *acutangula* throughout their ranges would be an important step toward a contemporary treatment of subg. *Limnochloa*.

Basic typification studies are necessary in most taxa in subg. *Limnochloa*. Indeed, critical comparison of all names available for each taxon is poorly documented in the literature. It is doubtful that any worker has recently critically examined and compared type specimens, and there is little indication that Svenson had all these types available to him during his study of *Eleocharis*.

RESEARCH OBJECTIVES

The primary objectives of this research were to review certain problematic taxa of *Eleocharis* subg. *Limnochloa* in order to define species clearly, revise nomenclature, and provide a taxonomic treatment. Species names studied during the course of this research included *E*. *acutangula*, *E*. *fistulosa*, *E*. *planiculmis* Steud., *E*. *obtusetrigona*, *E*. *strobilacea* Pedersen, (the *E*. *acutangula* complex), *E*. *austro-caledonica*, *E*. *cellulosa*, *E*. *compacta* R. Br., *E*. *mutata*, *E*. *scariosa* Steud., *E*. *spiralis*., *Scirpus acutetrigonous* Salzm *ex* Steud., and *Scirpus dictyospermus* Wright (the *E*. *mutata* complex). Results were derived from a morphological study based on the examination of more than 2300 specimens (including types) from 35 herbaria, supplemented with field studies in the southeast United States and Mexico. An enumeration of the specific problems investigated follows:

1. SEM examination of achene gross- and micromorphology
2. Taxonomic study of the worldwide variation of *E*. *mutata*

3. Taxonomic study of the relationship of *E*. *spiralis*, *E*. *austro-caledonica*, and *E*. *compacta* to each other and to *E*. *mutata*
4. Taxonomic study of the variation of *E*. *cellulosa* throughout its range
5. Taxonomic study of the worldwide variation of *E*. *acutangula*, and its relationship to *E*. *fistulosa*, *E*. *neotropica* sp. nov., *E*. *planiculmis*, *E*. *obtusetrigona*, *E*. *steinbachii* sp. nov., and *E*. *strobilacea*
6. Nomenclatural history and lectotypification

This research concludes with a taxonomic treatment of the taxa studied including necessary typification, updated or clarified synonymy, ecological data, and extensive specimen citations.

CHAPTER II

ACHENE MORPHOLOGY OF SELECTED SPECIES OF *ELEOCHARIS* SUBG. *LIMNOCHLOA*

INTRODUCTION

Examination of achene micromorphology by scanning electron microscopy (SEM) has been widely employed in taxonomic study of several genera of Cyperaceae (e.g., Schuyler 1971; Wujek et al. 1992; Strong 2006), and particularly in sectional studies of *Carex* (e.g., Waterway 1990; Rettig 1990). Menapace (1991b) published the first extensive report of the utility of achene micro-morphology as an aid in systematics in *Eleocharis*, especially its potential in assigning sectional or serial rank. Menapace (1993) was also able to place species of *Eleocharis* at the series level previously unassigned by Svenson (1939) based on differences in achene micromorphology. Menapace (1991b) indicated that the characteristics of the inner periclinal and anticlinal cell walls could prove important in assessing taxonomic relationships within *Eleocharis* subg. *Limnochloa*. Although there are now a host of published studies of achene micromorpholgy of various taxa in Cyperaceae, few could be located depicting micrographs of *Eleocharis* subg. *Limnochloa*. Two of the taxa treated herewith, *E*. *acutangula* and *E*. *cellulosa*, were examined by Varma et al. (1989) and Menapace (1991b) respectively, but without comparisons from throughout their ranges. No published studies comparing achene micromorphology between infraspecific taxa in *Eleocharis* could be located. The gross morphology and micromorphological characters of epidermal cells of mature achenes were studied using SEM as an initial part of the systematic study of the taxa treated. In addition to very high magnification for study of micromorpholgy, SEM is also useful in study of gross morphology of achenes in Cyperaceae because it has the additional advantage of producing images with very great depth of field when compared to light microscopy. Thus, SEM could prove to be especially useful for discovering new characters, and for critical examination of topographical features of the mature fruit previously known to be important in the taxonomy of *Eleochairs*. Characters know to be particularly useful in distinguishing closely related species in subg. *Limnochloa* include perianth bristle texture and vestiture, the nature and degree of achene sculpturing, epidermal cell shape, and details associated with the tubercle.

MATERIALS AND METHODS

Mature achenes were removed from the middle of a spikelet of representative herbarium specimens from throughout the geographic range of each taxon (Table 1). For examination of gross morphology and micromorphology, one and four dried achenes from each accession respectively were mounted on 10 mm diameter SEM stubs using conductive 8 mm wide double-sided adhesive carbon tape (Electron Microscopy Sciences #77816), and coated with 400 Å (1 Å = 0.1 nm) of gold-palladium applied in 5-s bursts at 10 milliamps using a Hummer I Sputter Coater. Achene epidermal cells are visible through the transparent periclinal layer when examined with light microscopy. However, these cells are completely obscured when examined using secondary and backscattered electron images produced by SEM. Therefore, for examination of achene micromorphology, prior to mounting, the cuticle and outer periclinal cell wall layer were removed using a procedure slightly modified from Schuyler (1971) as follows: achenes were acetolyzed by soaking in approximately 10 ml of a 9:1 mixture of acetic anhydride and sulfuric acid for 10-24 hours in 15 ml screw top test tubes. The test tubes with achenes were then briefly sonicated in order to loosen and remove the remaining debris. The solution was then decanted, and the achenes rinsed three times with 20 ml of distilled water, placed on filter paper on a watch glass, and allowed to air-dry in a desiccator for at least 24 hrs.

Table 1. Specimens examined using scanning electron microscopy.

Species	Specimens Examined
Eleocharis acutangula sensu lato	**NORTH AMERICA. U.S.A. Florida**. Lee Co.: about 2.5 air miles SW of the intersection of Hwy 82 and Green Meadows Rd, SE of Fort Myers, 12 Nov 2004, *Rosen & Carter 3206* (MICH). **CENTRAL AMERICA. El Salvador. Ahuachapan.** Lagunita las Ninfas, Apaneca, 28 Jan 1951, *Fassett 28721* (GH). **SOUTH AMERICA.** **Bolivia. Depart. Santa Cruz.** Lagunas pandas, Campos B.-Vista, Prov. Sara, 450 m, 24 Jan 1926, *Steinbach 7444* (MO). **Brazil. Minas Gerais.** road between Varginha to Eloi Mendas, 07 Feb 1970, *Koyama et al. 13704* (MICH). **Peru. Dpto. Loreto, Prov. Maynas.** Without location, 03 Aug 1967, *Torres 340* (GH); Maynas, Iquitos, prolongacion Yavari, Versailles-Paina, 23 Mar 1974, *McDaniel & Rimachi 18552* (MO). **AFRICA. Madagascar. Fianarantsoa.** Ambatofinandrahana, Itremo, petite vallee a l'ouest du Massif de l'itremo, 1680 m, 26 Nov 1993, *Du Puy & Andriantiana 2429* (MO); Marais de Didy, voir Joncacee de a a 2m, 21 Feb 1943, *Cours 1758* (P). **South Africa. Natal.** Greater Durban area, Mlazi Valley, 29^{o}54'S; 30^{o}49'E, 15 Mar 1992, *Ward 11925* (PRE). **Sudan.** Seriba Ghassas, Reise nach Central-Africa in Auflrafe der Humboldt-Stifsung, in Lande der Djur, 1 Sep 1869, *Schweinfurth 2326* (GH, Z). **ASIA. India. Karnataka. Hassan District.** Near Station, Hassan 10 Nov 1971, *Hooper & Gandhi 2373* (MO). **Vietnam. Quang Nam-Dà Nang. Tinh Prov.** Annam, Mount Bani, in the main coast range about 25 km from Tourane (Da Nang), May-Jul 1927, *Clemens & Clemens 4050* (F).

Table 1. *Continued*

Eleocharis cellulosa	**NORTH AMERICA. U.S.A. Florida**. Lee Co.: Wild Turkey Strand Natural Area, about 2.5 air miles SW of the intersection of Hwy 82 and Green Meadows Rd, SE of Fort Myers, 12 November, 2004, *Rosen & Carter 3208* (MICH). **Texas**. Calhoun Co.: S of Hwy 185, 4.1 miles E of Seadrift, 24 Jul 2004, *Rosen & Combs 3018* (MICH). **MEXICO. Campeche.** Canal de la Laguna El Vapor, El Carmen, 26 Oct 1989, *Ocana-Nava & Coronado 342* (MEXU). **CARIBEAN BASIN. Bahamas. New Providence.** off Coral Harbour Road near airport, 07 Jun 1979, *Correll 50733* (NY).
Eleocharis mutata	**NORTH AMERICA. U.S.A. Texas**. Brazoria Co.: Hoskin's Mound within the Brazoria National Wildlife Refuge, 3.8 km SE of the intersection of FM 2004 and Co. Rd 277, 29 Aug 2003, *Rosen & Jones 2614* (MICH). **MEXICO. Jalisco.** About 2 km N of Puerto Vallarta W of the airport, 13 Nov 1963, *Feddema 2533* (MICH). **CENTRAL AMERICA. Nicaragua.** Department of Zelaya, Corn Island, 06 Mar 1971, *Svenson 4317* (BRIT). **SOUTH AMERICA. Venezuela. Sucre.** Laguna Litorales de Cumana, 20 Jan 1974, *Campos 522* (US). **AFRICA. Togo.** Agwegan, entre route et lagune, depression sale, savane herbense inonde eau sale 9 gr Natt/litre., 26 Jun 1985, *Schafer 8629* (US).

Table 1. *Continued*

Eleocharis obtusetrigona	**NORTH AMERICA. MEXICO. Veracruz.** Miradores, municipio de Dos Rios, dentro del agua de la presa, 14 Oct 1974, *Ventura 10639* (WIS). **SOUTH AMERICA. Paraguay.** La Soledad, Santiago, Misiones, shallow water, 23 Dec 1965, *Pedersen 7634* (C).
Eleocharis spiralis	**ASIA. Malaysia. Sabah, British North Borneo,** Mount Kinabula, Jesselton 14-18 Dec 1915, *Clemens 9716* (K). **Sri Lanka. Amparai District.** Tandiadi Kalapu lagoon, S of Mile 215 on Rd A 4, 07 Feb 1971, *Koyama et al*. *14014* (GH). **OCEANIA. AUSTRALIA. Northern Territory.** Darwin, Adelaide River floodplain, Arnhem Hwy, 12^o 41' S 131^o 21' E, 17 Apr 1980, *Rankin 2255* (BRI). **PAPUA-NEW GUINEA**. **Morobe District.** Lae, T.N.G., lat 6^o 47’ S, long 147 ^{o} 00’ E, 28 Nov 1963, *Womersley19043* (GH).

In some cases, it was necessary to roll the achenes on Scotch® permanent double-sided tape using light finger pressure in order to remove the loosened periclinal layer. Achenes were examined using a JEOL 6400 Scanning Electron Microscope at an accelerating voltage of 15 KV at a wide range of magnifications (35×-1800×) and working distances, and micrographs prepared using Polaroid Polapan 400 ISO 400/27° film. When examining micromorphology, it was determined that variation of epidermal cell shape within an accession was minimal when examining homologous regions on the achenes. Among achenes from the same accession, angles and bases were the most variable. Faces of achenes near the median longitudinal plane were the least variable; therefore, all observations for comparison and micrographs are from that region. Micrographs and descriptions are provided, and terminology follows Radford et al. (1974) and Stearn (1992). For consistency, some terms specific to achenes of *Eleocharis* were taken from González-Elizondo (2002).

RESULTS AND DISCUSSION

Achene Gross Morphology of *Eleocharis mutata* Complex

Specimens of *Eleocharis mutata* were examined from the United States, Mexico, Central America, South America, and Africa (Table 1). Micrographs depicting the range of variation in achene gross morphology throughout the distribution of *E*. *mutata* are provided in Fig. 1 and Fig. 2. Perianth bristles (Fig. 1A) appear to be in two series and are narrow to strap shaped, curved ascending to sometimes tortuous, and range in length from just above the middle of the achene to well above the tubercle (Fig. 1A). The perianth bristles are coarsely retrorsely spinulose from the tip to just below the middle or rarely nearly to the base. *Schafer 8629* from Africa (Fig. 1E) is exceptional with only a few short, salient retrorse spinules near the bristle apex. Achenes are compressed to sub-compressed biconvex and range in shape (not including the annulus or tubercle) from obpyriform to obovate. Achene surfaces appeared smooth to longitudinally ridged. Annulus (Fig. 1A) shape is typically transversely oblong and sometimes tapers apically. In cross section, annulus shape ranges from transversely elliptic to transversely rhombic, although this character proved very difficult to access when viewed with a dissecting microscope. Tubercle shape and prominence were found to be quite variable. When well defined they range in outline from very shallowly triangular to triangular. However, in some specimens they appear withered and nearly absent (e.g., Fig. 2A).

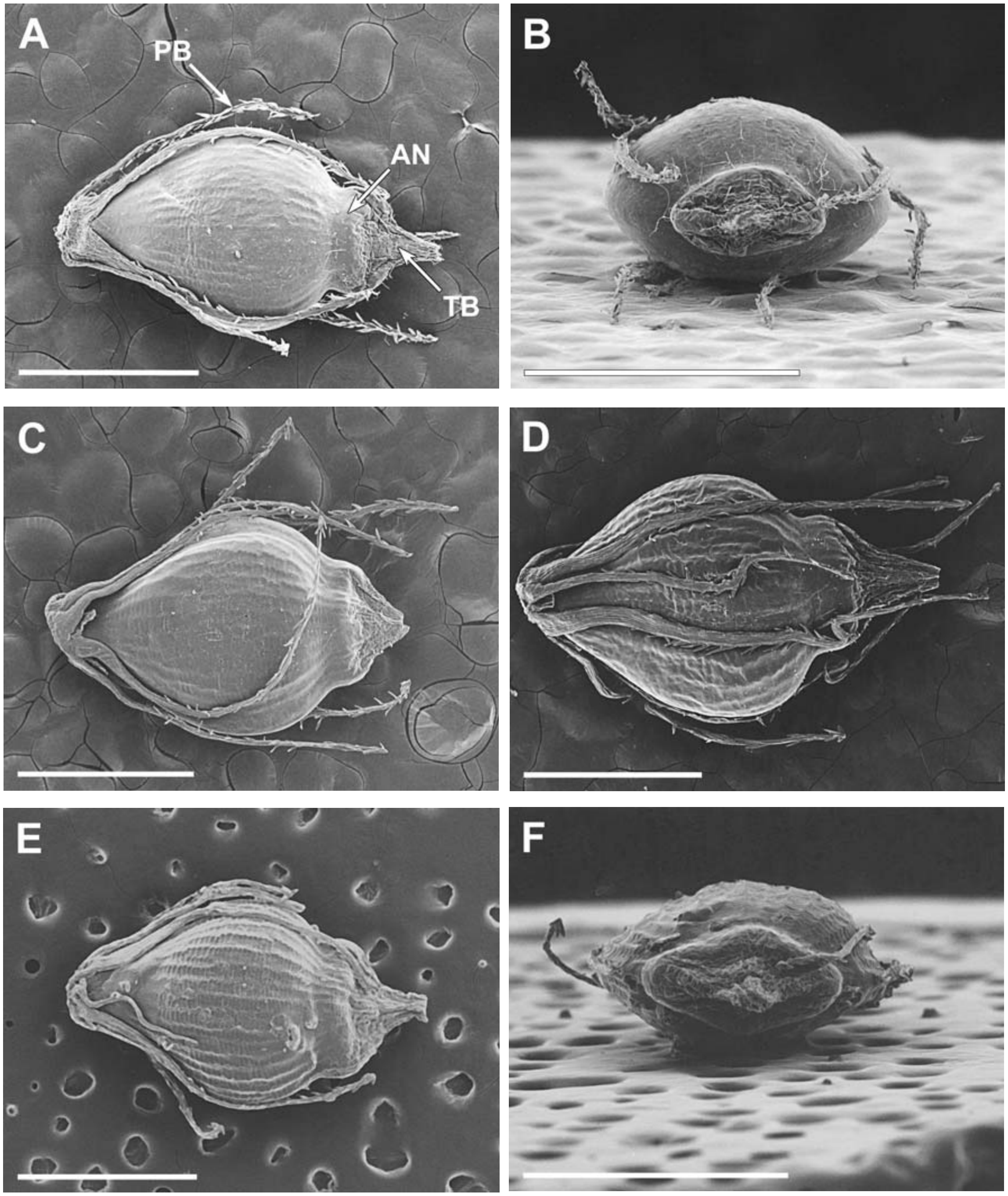


Fig. 1. SEM micrographs of achenes of representative specimens of *Eleocharis mutata*. A-B. Venezuela (*Campos 522*). C. Mexico (*Feddema 2533*). D. United States (*Rosen & Jones 2614*). E-F. Africa (*Schafer 8629*). AN = annulus; PB = perianth bristles; TB = tubercle; scale bars 1 mm.

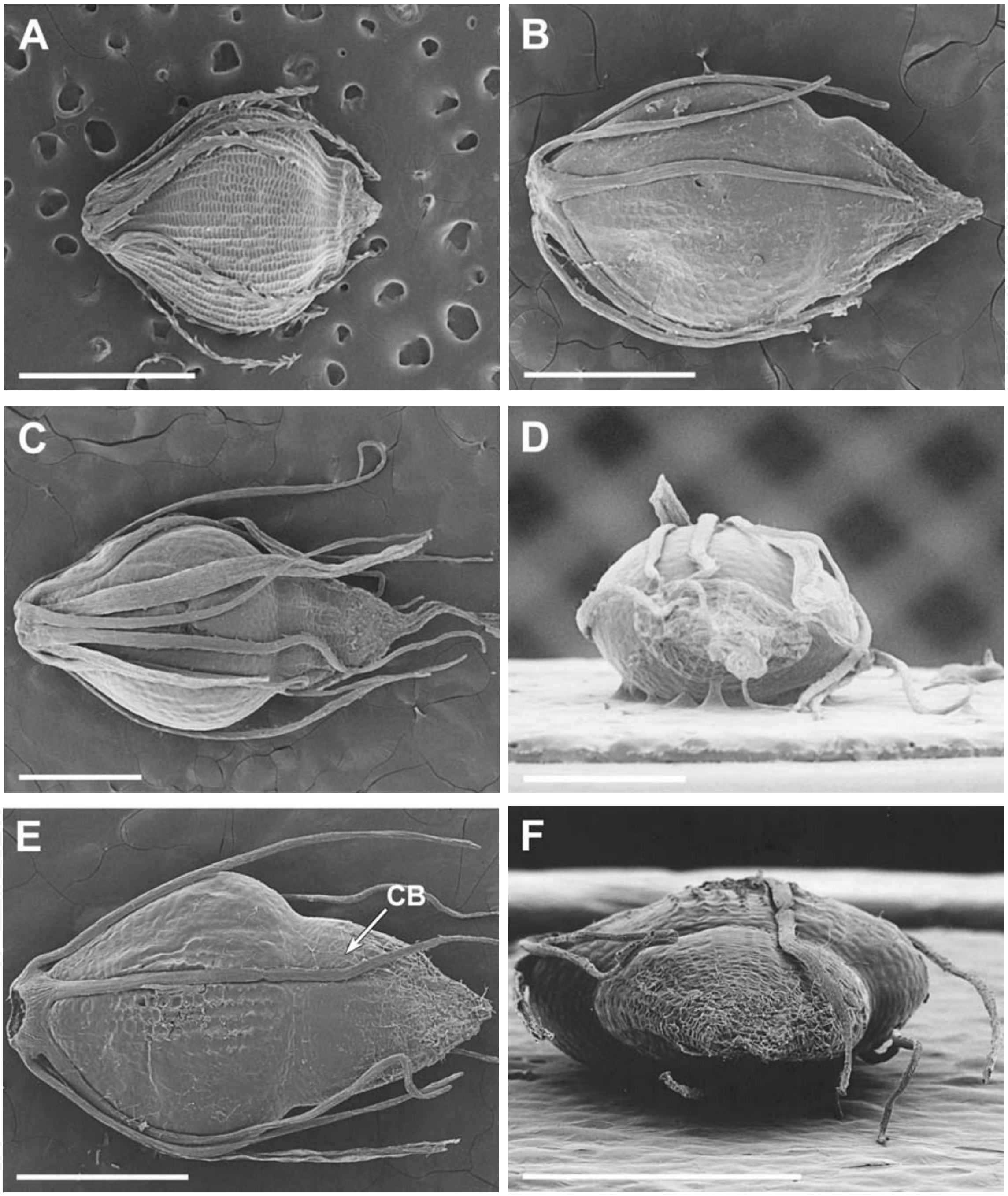


Fig. 2. SEM micrograph of achenes of representative specimens of *Eleocharis mutata* and *E*. *cellulosa*. A. *E*. *mutata*, Nicaragua (*Svenson 4317*). B-F. *E*. *cellulosa*. B. Mexico (*Ocana-Nava & Coronado 342*). C-D. Bahamas (*Correll 50733*). E-F. United States (*Rosen & Combs 3018*). CB = conical beak; scale bars 1 mm.

Excellent examples of the later condition are also depicted in Browning et al. (1997; Fig. 5A) and Fernald (1925; plate 149-14).

Specimens of *Eleocharis cellulosa* were examined from the United States, Mexico, and the Caribbean Basin (Table 1). Micrographs depicting the range of variation in achene gross morphology throughout the distribution of *E. cellulosa* are provided in Fig. 2. Perianth bristles appear to be in two series (although this condition is hard to interpret in some specimens) and are narrow, curved ascending to sometimes tortuous and range in length from just above the summit of the achene to just above the tubercle. In *Rosen & Combs 3018* from the United States (Fig. 2E), the bristles appear to arise from a conspicuous basal ring. Perianth bristles are smooth, or rarely minutely spinulose (seen only at high magnification). However, a Caribbean specimen (*Correll 50733*, Fig. 2C) has perianth bristles that are conspicuously retrorsely spinulose from the tip to just below the middle, are strap shaped, and are very similar to specimens of *E. mutata*.

Achenes are compressed to sub-compressed biconvex, and range in outline (not including the conical beak or tubercle) from widely obovate to very widely obovate (widely elliptic in *Ocana-Nava & Coronado 342* from Mexico; Fig. 2B). Achene surfaces are smooth, and the conical beak (Fig. 2E) and tubercle form a complex that is variable. In *Rosen & Combs 3018* from the United States (Fig. 2 E-F), the conical beak and tubercle are not readily distinguishable.

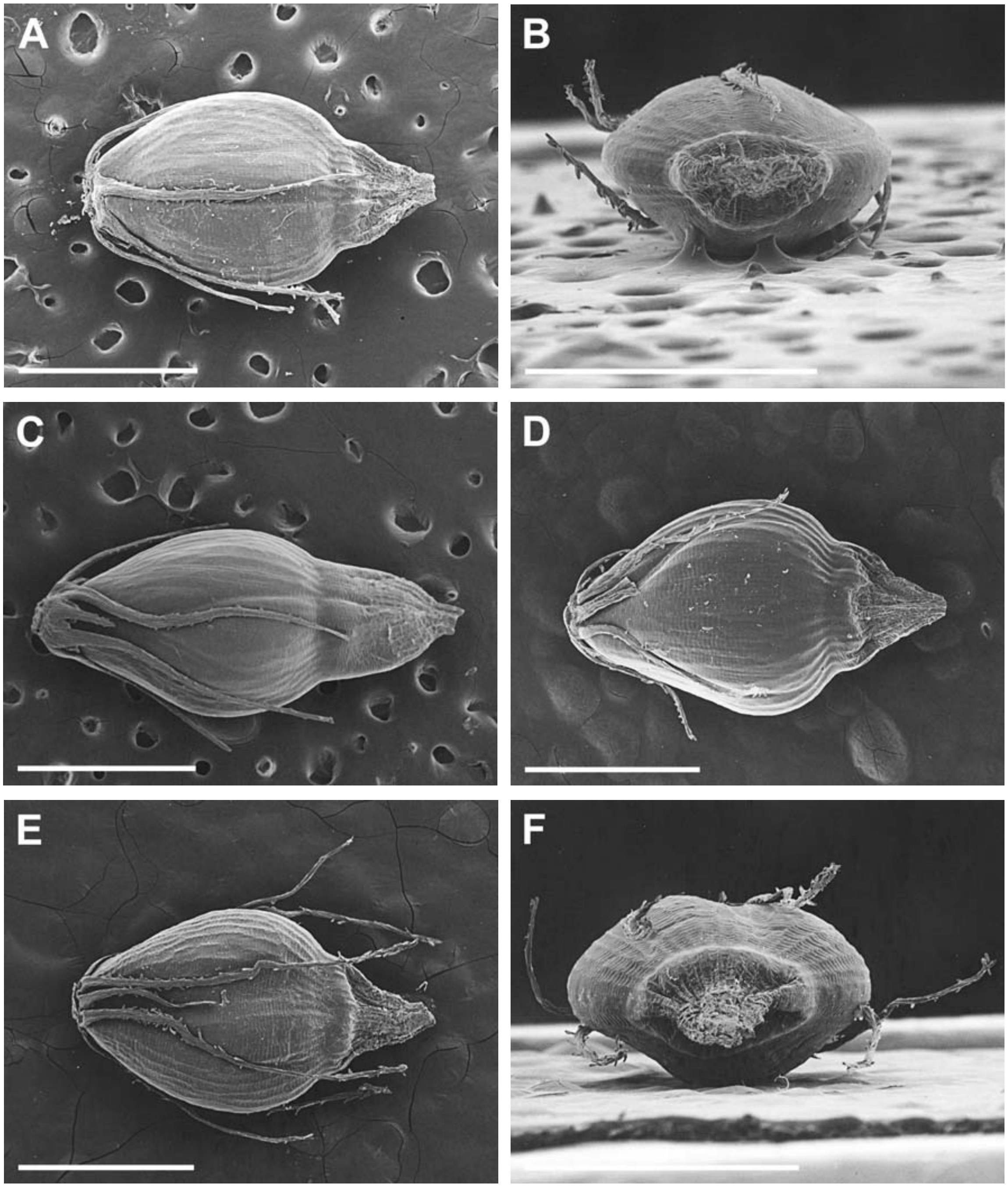


Fig. 3. SEM micrographs of achenes of representative specimens of *Eleocharis spiralis*. A-B. Malaysia (*Clemens 9716*). C. Sri Lanka (*Koyama 14014*). D. Australia (*Rankin 2255*). E-F. Papua-New Guinea (*Womersley19043*). Scale bars = 1 mm.

However, varying degrees of distinction can be seen between the conical thickening and tubercle in the other specimens (Fig. 2 B-D).

Specimens of *Eleocharis spiralis* were examined from Malaysia, Sri Lanka, Australia, and Papua-New Guinea (Table 1). Micrographs depicting the range of variation in achene gross morphology throughout the distribution of *E*. *spiralis* are provided in Fig. 3. Perianth bristles are narrow, straight-tortuous and typically range in length from just below the middle of the achene to just above the achene apex, although in *Womersley 19043* from Papua-New Guinea perianth bristles reach the tip of the tubercle (Fig. 3 E). Perianth bristles are smooth to irregularly spinulose from the tip to just below the middle or rarely nearly to the base, and the spinules are variously antrorse, retrorse, or squarrose, with sometimes all three states occurring on the same bristle.

Achenes are biconvex with a central bulge on the abaxial (?) side and range in shape (not including the annulus or tubercle) from obovate to broadly obovate. Achene surfaces are smooth to very finely longitudinally ridged. The annulus is transversely oblong and sometimes tapers apically. In some specimens (e.g. *Koyama et al*. *14014*, Fig. 3C), the constriction at the summit of the achene is prolonged and gradually tapers into a compressed conical beak similar to *E*. *cellulosa*. Rarely, both conditions occur on achenes from the same accession. In cross section, annulus shape is transversely elliptic. Tubercle shape is typically triangular except for *Koyama et al*. *14014* in which it is nearly absent (Fig. 3C).

Achene Gross Morphology of *Eleocharis acutangula* Complex

In specimens of the *Eleocharis acutangula* and *E*. *obtusetrigona*, the achene apex is markedly constricted to a short neck, although the neck is sometimes obscured by the tubercle and careful examination is required to distinguish this condition. In species of this complex, the tubercle does expand basally to form a rim, but the tissue is of the same color and texture as that of the style base, differing markedly from the *E*. *mutata* complex. Significant differences were observed amongst specimens examined referable to *E*. *acutangula* including the vestiture and length of the perianth bristles, and achene and tubercle shape.

Specimens of *Eleocharis acutangula* were examined from the United States, Central America, South America (Bolivia, Brazil, Peru), Africa (Madagascar, South Africa, Central African Republic), and Asia (India, Vietnam; Table 1). Micrographs depicting the range of variation in achene gross morphology throughout the distribution of *E*. *acutangula* are provided in Fig. 4-Fig. 6. Perianth bristles are in two series and are narrow to strap shaped, curved ascending (infrequently some tortuous), and range in length from just above the middle of the achene to well past the tubercle (rarely a few rudimentary).

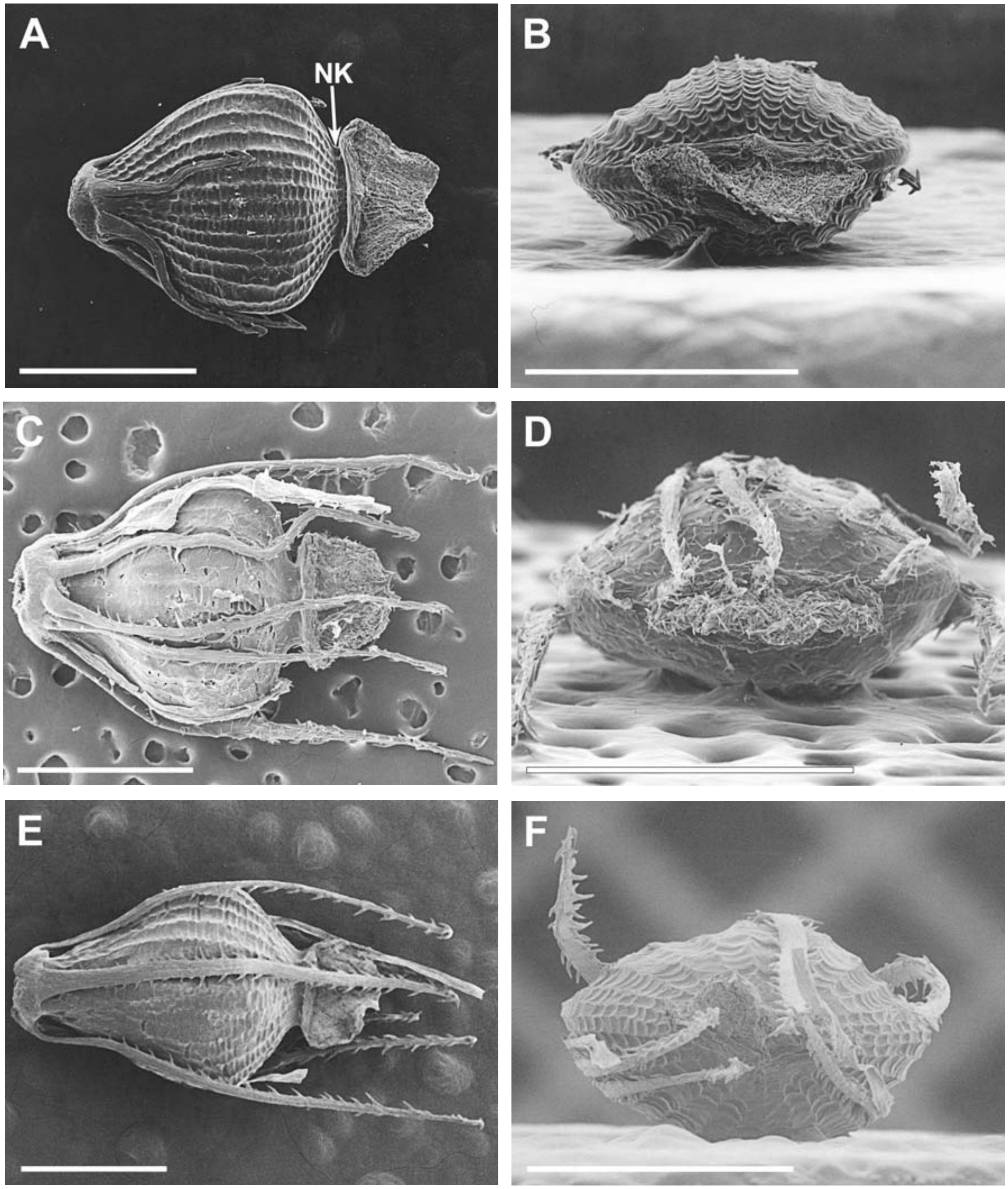


Fig. 4. SEM micrographs of achenes of representative New World specimens of *Eleocharis acutangula*. A-B. United Sates (*Rosen & Carter 3206*). C-D. El Salvador (*Fassett 28721*). E-F. Brazil (*Koyama et al. 13704*). NK = neck; scale bars 1 mm.

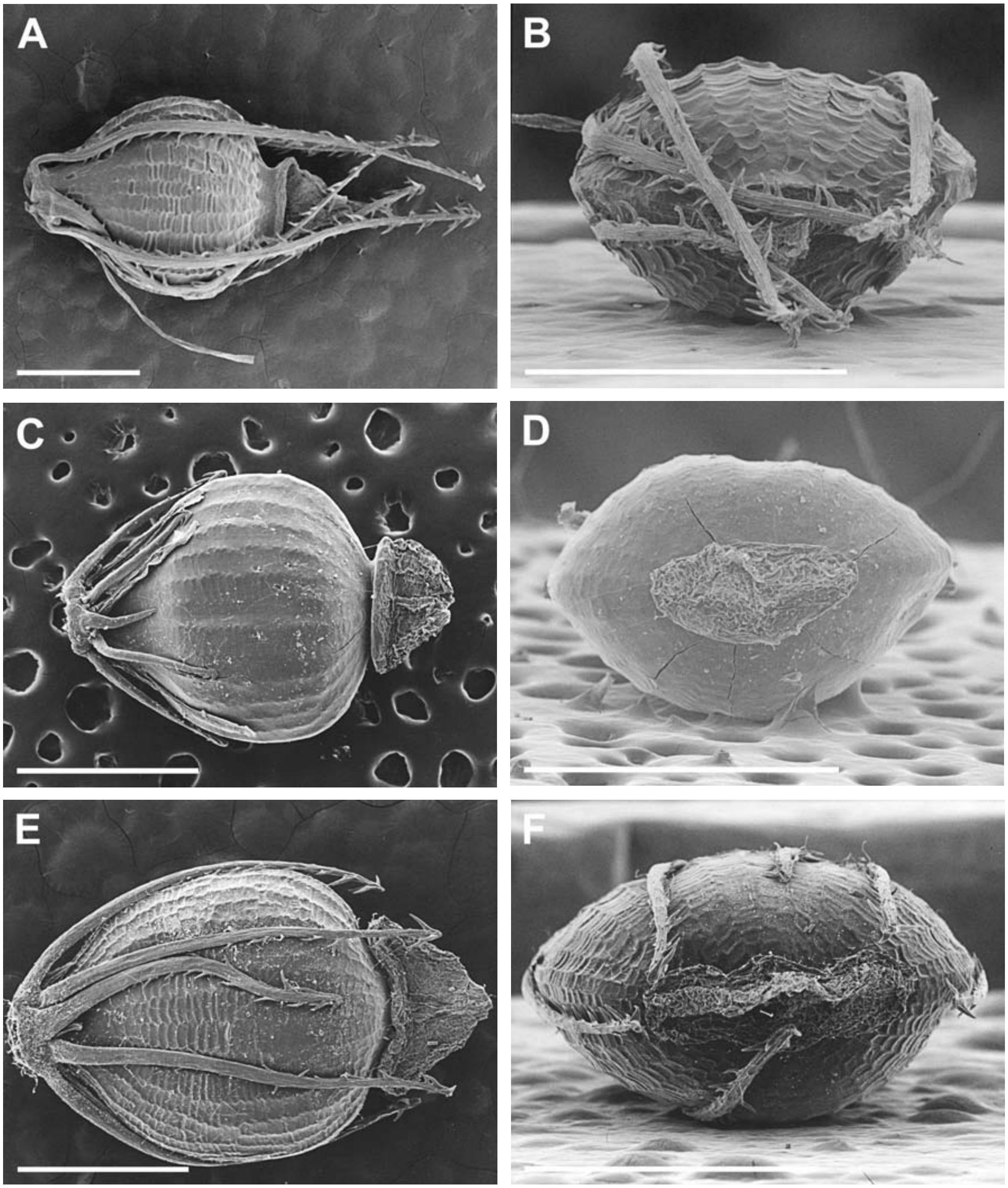


Fig. 5. SEM micrographs of achenes of representative Old World specimens of *Eleocharis acutangula*. A-B. Madagascar (*Du Puy & Andriantiana 2429*). C-D. South Africa, Natal (*Ward 11925*). E-F. Central African Republic (*Schweinfurth 2326*). Scale bars = 1 mm.

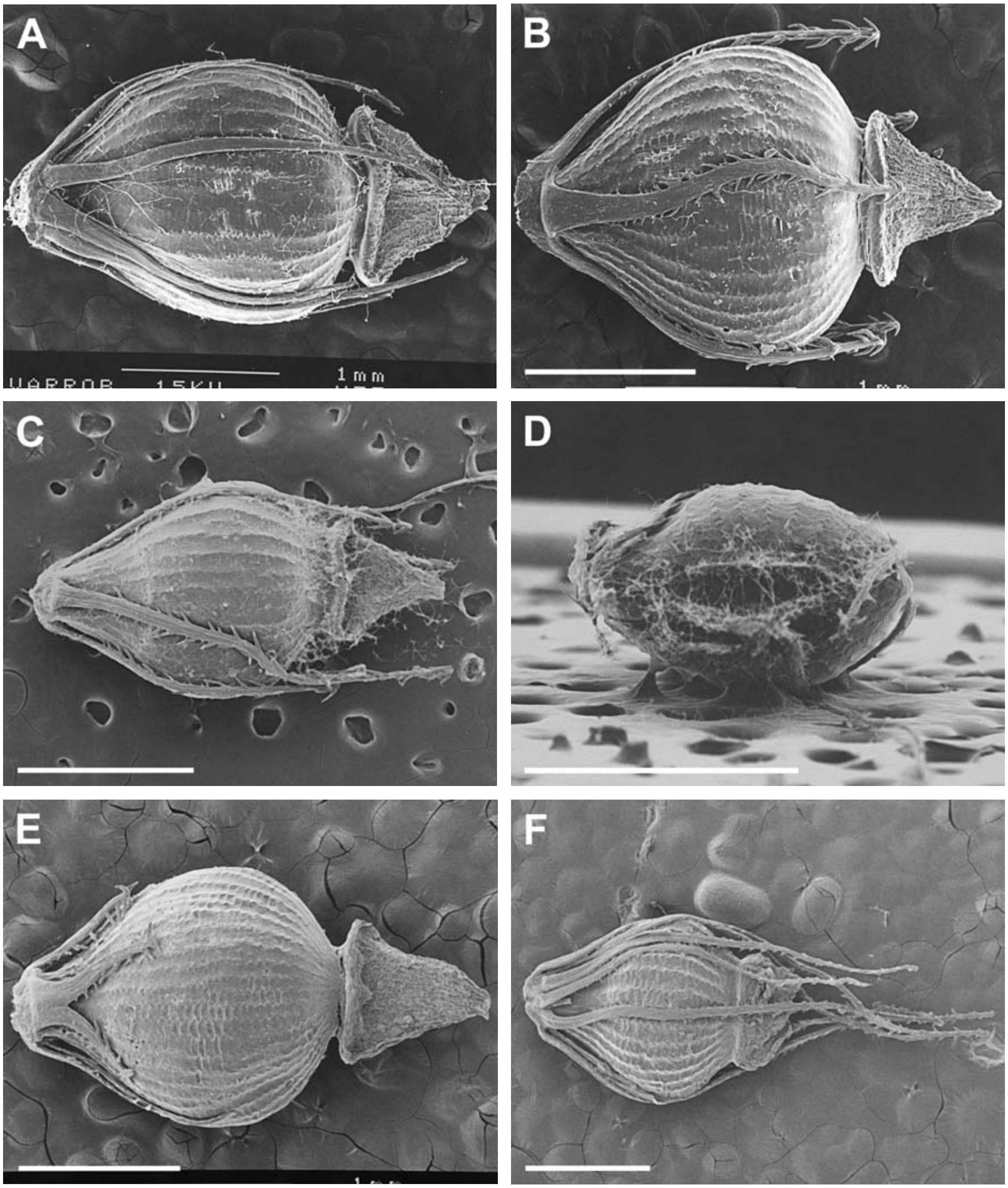


Fig. 6. SEM micrographs of achenes of representative specimens of *Eleocharis acutangula*, *E*. *steinbachii*, and *E*. *neotropica*. A-D. *E*. *acutangula*, Central African Republic (*Schweinfurth 2326*; smooth bristle variant from Z). B. India (*Hooper & Gandhi 2373*). C-D. Vietnam (*Clemens & Clemens 4050*). E. *E*. *steinbachii* (*Steinbach 7444* from Bolivia). F. *E*. *neotropica* (*McDaniel & Rimachi 18552* from Peru). Scale bars = 1 mm.

Two conditions occur in the surface vestiture of perianth bristles in *E*. *acutangula*. In the first and by far the most common, perianth bristles that range in length from just past the summit of the achene body to well above the tubercle are coarsely retrorsely spinulose from the tip to just below the middle or rarely nearly to the base. In the second, achenes of specimens from the United States (*Rosen & Carter 3206*; Fig. 4A) and South Africa (*Ward 11925*; Fig. 5C) have perianth bristles shorter than the achene body with only a few short, salient retrorse spinules near the apex of the bristles. In examining multiple achenes from a single accession or achenes from duplicates of the same collection, the length and texture of perianth bristles was less variable than the degree or presence of vestiture. For example, in *Schweinfurth 2326* from the Central African Republic (the “type” of *E*. *fistulosa* var. *robusta* Boeckeler), achene bristles vary from retrorsely spinulose (Fig. 5E) to smooth (Fig. 6A).

Achenes (not including the tubercle) are compressed to sub-compressed biconvex and range from obovate to obpyriform or widely obovate. Achene surfaces are faintly to prominently longitudinally ridged, and the overall surface is more coarsely sculptured or areolate than the preceding taxa due to raised vertical and horizontal anticlinal walls of the epidermal cells. Exceptionally, the achenes from a South African specimen (*Ward 11925*) are somewhat smooth (Fig. 5 C-D). In *E*. *acutangula*, the tubercle is more prominent than in the preceding species complex, and its shape is variable.

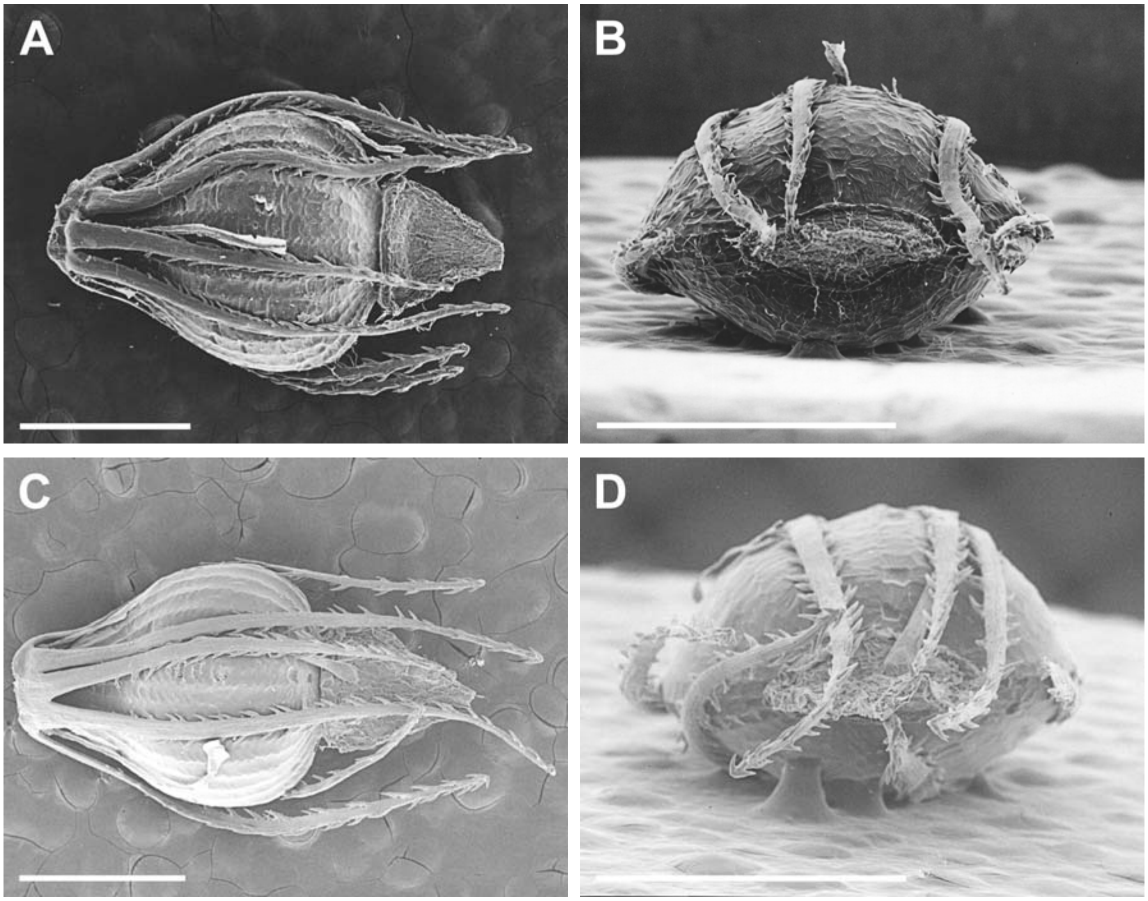


Fig. 7. SEM micrographs of achenes of representative specimens of *Eleocharis obtusetrigona*. A-B. Mexico (*Ventura 10639*). C-D. Paraguay (*Pedersen 7634*). Scale bars = 1 mm

The tubercle is typically well defined, dorsoventrally compressed, and ranges from very shallowly triangular to deltate. In some specimens, the apex of the tubercle appears to be truncate or occasionally emarginate (Fig. 4A, E). The summit of the achene was consistently constricted into a neck-like region in all specimens examined, although the ratio of the constriction to the width of both achene and tubercle is variable (e.g., Fig. 4C vs. 6F). While examining achenes of specimens referable to *E*. *acutangula*, two novelties from South America were discovered; *E*. *steinbachii* sp. nov. (Fig. 6E), and *E*. *neotropica* sp. nov. (Fig. 6F). At least two infraspecific taxa within *E*. *acutangula* are also apparent.

Specimens of *Eleocharis obtusetrigona* were examined from Mexico and South America (Paraguay; Table 1). Micrographs depicting the range of variation in achene gross morphology throughout the distribution of *E*. *obtusetrigona* are provided in Fig. 7. Perianth bristles are stiff, strap shaped, ascending, and extended to just below the summit of the tubercle to well above it. The perianth bristles are coarsely retrorsely spinulose from apex nearly to base.

Achenes are sub-compressed biconvex and obpyriform, and achene surfaces are prominently longitudinally ridged and coarsely sculptured areolate to alveolate. The tubercle is dorsoventrally compressed and deltate. Achenes of *E*. *obtusetrigona* are the least variable of all taxa examined.

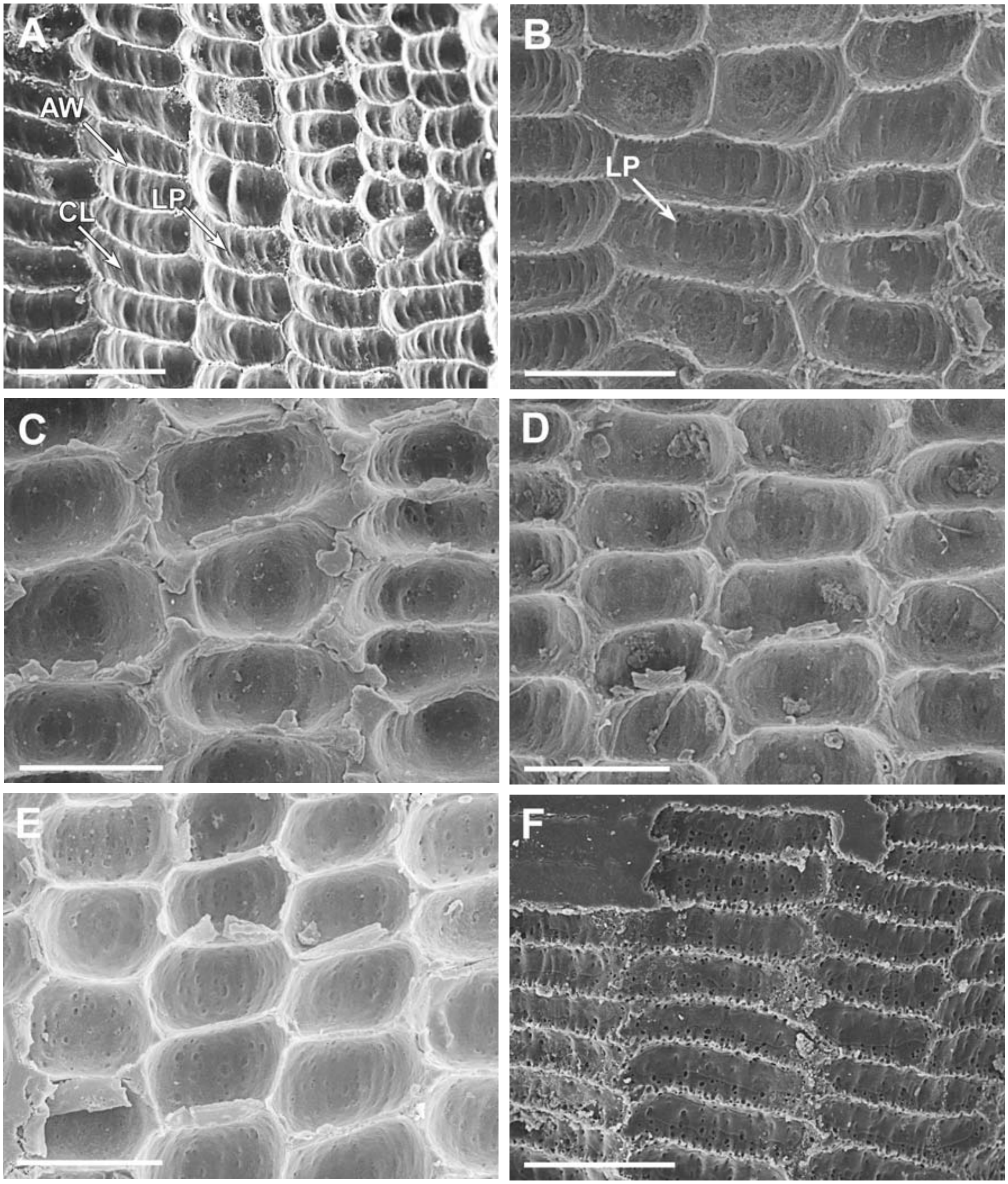


Fig. 8. SEM micrographs of achene micromorphology of *Eleocharis mutata*, *E*. *cellulosa*, and *E*. *spiralis*. A-B. *E*. *mutata*; A. Mexico (*Feddema 2533*); B. United States (*Rosen & Jones 2614*). C-E. *E*. *cellulosa*; C. Bahamas (*Correll 50733*); D. Mexico (*Ocana-Nava & Coronado 342*); E. United States (*Rosen & Carter 3208*). F. *E*. *spiralis*; Australia (*Rankin 2255*). AW=anticlinal wall; CL=cell lumen; LP=lumen pit; scale bars = 0.1 mm.

Achene Micromorphology of *Eleocharis mutata* Complex

Achene micromorphology in *Eleocharis mutata*, *E*. *cellulosa*, and *E*. *spiralis* is similar in concave and distinctly and deeply undulating inner periclinal walls and usually numerous lumen pits (Fig. 8 A-F). Upon careful inspection at high magnification, the anticlinal walls are entire to sinuulate in *E*. *mutata* (particularly at the base of the wall), entire in *E*. *cellulosa*, and sinuulate in *E*. *spiralis*. Acetolysis of achenes of *E*. *spiralis* was difficult. Two extremes seemed to occur after trials for varying time durations (12, 24, and 48 hours). Either the periclinal layer remained intact following acetolysis and sonication, or when it was exfoliated, the underlying cell ultrastructure was destroyed. This suggests that the cuticle and periclinal wall are much harder than the underlying cell walls. Only one satisfactory specimen of *E*. *spiralis* was obtained and examined. Achene epidermal cell shape varies among *E*. *mutata*, *E*. *cellulosa*, and *E*. *spiralis*. In *E*. *mutata*, the polygonal cells are transversely oblong in shape; however, apparently rarely when an epidermal cell divides twice, resulting daughter cells are transversely widely oblong to square. In *E*. *cellulosa*, the polygonal cells are transversely oblong or more commonly transversely widely oblong and appear to be deeply pitted when viewed with a dissecting microscope. In *E*. *spiralis*, the polygonal cells are narrowly transversely oblong.

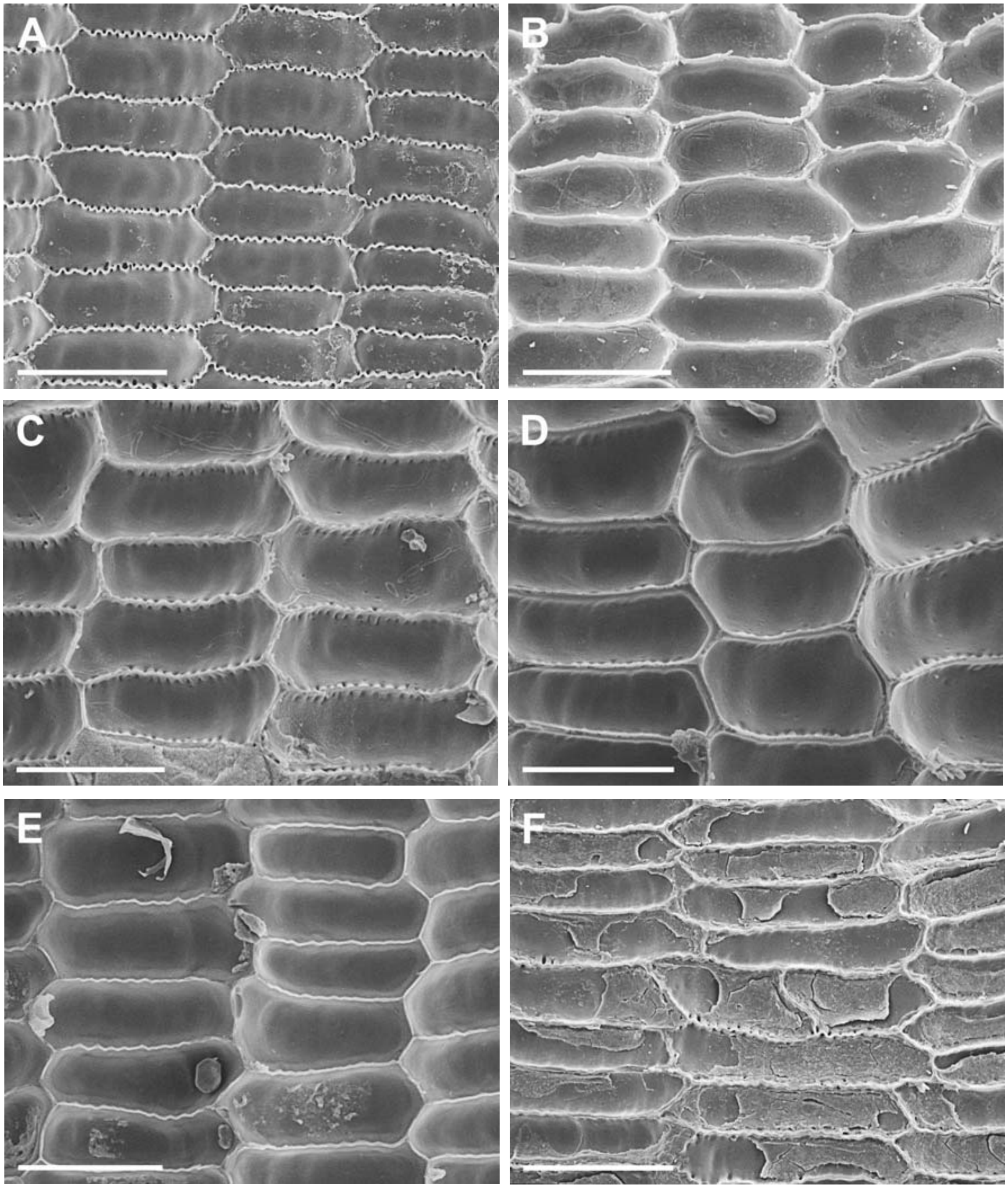


Fig. 9. SEM micrographs of achene micromorphology of *Eleocharis acutangula*. A. United Sates (*Rosen & Carter 3206*). B. El Salvador (*Fassett 28721*). C-D. Peru (*Torres 340 = E. neotropica*). E. Madagascar (*Du Puy & Andriantiana 2429*). F. Central African Republic (*Schweinfurth 2326*). Scale bars = 0.1 mm.

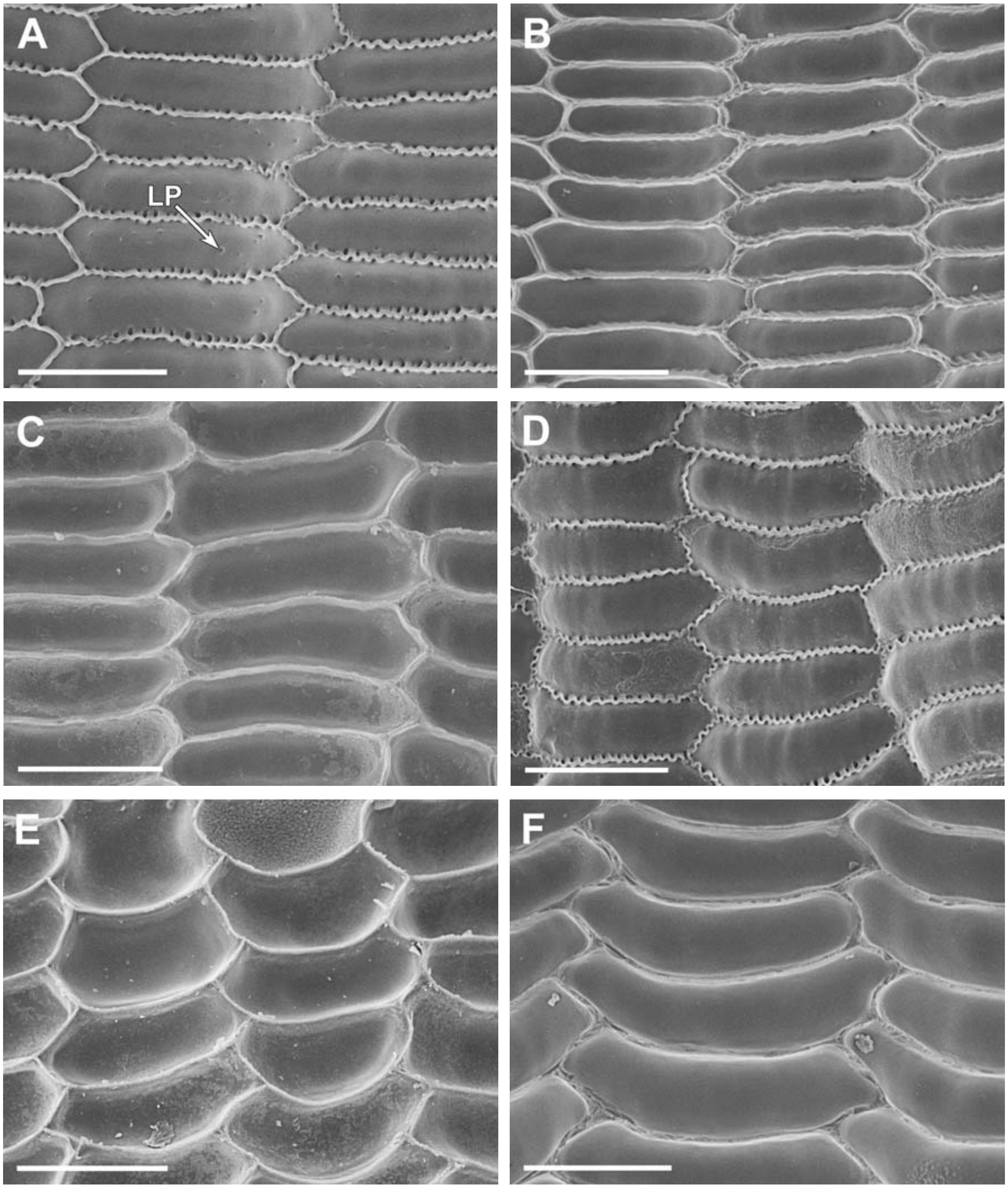


Fig. 10. SEM micrographs of achene micromorphology of *Eleocharis acutangula* and *E. obtusetrigona*. A-D *E*. *acutangula*; A-B. South Africa, Natal (*Ward 11925*). C. India (*Hooper & Gandhi 2373*). D. Vietnam (*Clemens & Clemens 4050*). E-F. *E*. *obtusetrigona*. E. Mexico (*Ventura 10639*). F. Paraguay (*Pedersen 7634*). LP=lumen pit; scale bars = 0.1 mm.

Achene Micromorphology of *Eleocharis acutangula* Complex

Substantial variation in achene micromorphology was observed in specimens referable to *Eleocharis acutangula*, and in some cases, among achenes of the same accession (Fig. 9; Fig. 10 A-D). Differences occurred in the surface topography of the inner periclinal walls, the occurrence of lumen pits, the marginal shape and thickness of anticlinal walls, and achene epidermal cell shape. The inner periclinal walls are concave and range from shallowly undulating (e.g. Fig. 9A) to smooth (e.g. Fig. 9B); however, this condition does not appear to vary among achenes of the same accession. In the South Africa specimen, *Ward 11925*, some very fine lumen pits were observed, but this was not consistent in all samples examined from the same accession (Fig. 10A-B). In other specimens with distinctly sinuulate anticlinal walls, lumen pits are observed at the bases of the walls. The anticlinal walls range in appearance from entire to markedly sinuulate, although this condition does not appear to have a geographic basis and, indeed, varies in different samples from the same accession (e.g. Fig. 9 C-D; Fig. 10 A-B). The anticlinal walls appear thickened in all specimens except *Du Puy & Andriantiana 2429* from Madagascar. In *E. acutangula*, the polygonal cells range in shape from transversely oblong to narrowly transversely oblong.

The achene micromorphology of *Eleocharis obtusetrigona* was found to be quite consistent and was least variable of all species studied. The inner periclinal walls are deeply concave and flat, and the anticlinal walls are entire

(Fig. 10 E-F). The achene epidermal cells are polygonal, and the shape is decidedly transversely oblong with most centrally located cells being reniform-upwardly curved (Fig. 10 E-F).

CONCLUSION

This is the first SEM study of variation in achene macro- and micromorphology in *Eleocharis* from a wide geographic area. Achene gross morphology differs among the complexes studied chiefly in the nature of the constriction between the achene and style base (tubercle). In the *E*. *mutata* complex, the tubercle merges gradually to abruptly from an annular or conical thickening at the apex of the achene. In the *E*. *acutangula* complex, the achene apex is markedly constricted to a short neck. *Eleocharis mutata* and *E*. *spiralis* are very similar in gross morphology with the achene apex slightly constricted to more than half the width of the achene, broadening again into a distinct to sometimes indistinct annulus of similar texture. In *E*. *cellulosa*, and rarely in some specimens of *E*. *spiralis* (e.g. Fig. 3C), the constriction at the summit of the achene is usually less abrupt and prolonged and gradually tapered into a compressed conical beak, merging into a short, and sometimes indistinct lamelliform tubercle. Both macro- and micromorphological achene characters seem to support a close phylogenetic relationship of *E*. *mutata*, *E*. *cellulosa*, and *E*. *spiralis* as suggested by Svenson (1929), and their divergence from the *E*. *acutangula* complex.

Differences were observed in achene gross morphology within taxa referable to *E*. *acutangula*, including the morphology of perianth bristles, achene and tubercle shape, and shape of epidermal cells. These characters were useful in delimiting taxonomic segregates within *E*. *acutangula*. Variation in micromorphology was observed among achenes from the same accession in the *E*. *acutangula* complex. Characters such as the aspect of anticlinal wall margins are too variable to be of much taxonomic use. Indeed, few salient micromorphological characters could be found that seem to hold much promise in infraspecific systematic study of both complexes. In all taxa studied, the degree of surface sculpturing of the achenes varies when viewed with SEM. However, when viewed with a dissecting microscope, achenes appeared to be conspicuously sculptured due the longitudinal rows of deeply pitted cells underlying the clear perclinal layer. Both macro- and micromorphology of *E*. *obtusetrigona* support its distinctness as a species from *E*. *mutata* and *E*. *acutangula*.

Achene macro- and micromorphology indicate a relationship among the species of the *Eleocharis mutata* complex and their distinctness from the *E*. *acutangula* complex and support the placement of all taxa studied within subg. *Limnochloa*. All species studied share the following micromorphology: concave inner periclinal walls; entire to sinuulate anticlinal walls, lumen pits, and polygonal epidermal cells. Results of this study may be useful in elucidating the phylogeny of the subgenus; thus, the real utility of achene micromorphology in

Eleocharis may be at the infrageneric level as other workers have suggested (Tallent & Wujek 1983; Menapace 1993).

CHAPTER III

MORPHOMETRIC NUMERICAL STUDY OF WORLDWIDE VARIABILITY OF *ELEOCHARIS MUTATA*

INTRODUCTION

Systematic study of Cyperaceae is challenging given the scarcity of morphological characters typically available in less reduced angiosperms. The study of *Eleocharis*, one the most highly structurally reduced genera of Cyperaceae, provides additional challenges. Although the ultimate difficulty in taxonomic study in *Eleocharis* is perhaps realized when investigating closely related taxa or infraspecific variation, others have convincingly demonstrated the validity in recognition of infraspecific taxa among some widely distributed species of *Eleocharis* (Larson & Catling 1996; Gregor 2003).

Many vegetative characters (e.g., culm height, width, and cross-sectional shape; leaf sheath texture and structure; rhizome length and diameter) are highly plastic and, although of some use in *Eleocharis* to separate taxa along infrageneric lines, are of little or no use distinguishing infraspecific taxa. In the aquatic subg. *Limnochloa*, significant variation in culm anatomy as a response to environmental conditions (e.g., seasonal submersion) has been demonstrated within well defined species such as *E*. *cellulosa* (Edwards et al. 2003; Baksh & Richards 2006), which suggests that caution should be taken when considering vegetative characters for use in morphometric numerical study of closely related taxa of *Eleocharis*. Svenson (1929) emphasized achene characters and perianth bristle texture in differentiating species of *Eleocharis*. Svenson's (1929, 1957) keys separating members of series Mutatae included characters such as achene surface sculpturing or ornamentation, cellular shape; degree of constriction of achene summit; achene color and shape; and perianth bristle texture and dentation. A review of the literature reveals a tendency of workers investigating infraspecific variation in *Eleocharis* to rely primarily on characters and character states associated with the achene (Hines 1975; Żukowski & Klimco 1979; Catling 1994; Larson & Catling 1996; Gregor 2003). Indeed, achene-related characters are important in taxonomic limits in *Eleocharis* at all levels (Menapace 1991a). Larson and Catling (1996) satisfactorily separated *E*. *ovata* (Roth) Roem. & Schult. and *E*. *obtusa* (Willd.) Schult. based on tubercle width and the ratio of tubercle width to achene width. Gregor (2003) found stylopodium (tubercle) shape would distinguish *E*. *mamillata* Lindl. subsp. *austriaca* (Hayek) Strandhede from the nominal subspecies.

Eleocharis mutata is found in coastal habitats from southeast Texas, Mexico, Central America, tropical South America, the Caribbean Basin, and tropical Africa. Fernald (1925; plate 146, 11-14) indicated the need to investigate the variation in *E*. *mutata* observed in achenes of plants from French Guiana, the Galapagos Archipelago, Venezuela, and West Indies. Initial examination of numerous specimens in preparation for this study supports Fernald's evaluation. No study of the cosmopolitanism of *E*. *mutata* has been published. Browning et al. (1997) studied *E*. *mutata*, and considered it to be a hybrid involving *E*. *acutangula* and *E*. *dulcis*, apparently based on examination of only a few African specimens. Roalson (1999) suggested population studies were necessary to better understand *E*. *mutata* in Africa.

Stuessy (1990) recommends the use of multivariate statistics for study of infraspecific variation in vascular plants. Henderson and Ferreira (2002) used multivariate analysis to detect previously unknown infraspecific taxa in neotropical *Synechanthus* H. Wendl. (Arecaceae). Naczi et al. (1998) resolved the infraspecific variability of the *Carex willdenowii* Schkuhr *ex* Willd. complex by exploring multivariate data with principal components analysis (PCA). Previous workers have used PCA in order to detect infraspecific taxa from amongst specimens of a widely distributed or closely related species of *Eleocharis* and to extract variables with which to classify them (Gregor 2003).

The objective of this study was to determine if there is a practical infraspecific taxonomic separation to account for the morphological variability in *Eleocharis mutata* across its geographical distribution. Patterns in variation throughout the distribution of *E*. *mutata* may also aid in elucidating its evolutionary geography, nativity, and a pattern of introduction.

MATERIALS AND METHODS

Herbarium Selection

For this study, large domestic and foreign herbaria were selected that could provide loans yielding good geographical representation of *Eleocharis mutata*. Additional selection criteria included herbaria where types or otherwise notable specimens were housed as they came to light following an extensive literature review and correspondences with cyperologists worldwide. Svenson (1929) initially examined specimens from C, US, NEBC, NY, P, PH, S, and GH. In an attempt to better understand the limited resources available to him at that time, and the taxonomic decisions he made, specimens cited by Svenson for series *Mutatae* were re-examined.

Over 450 specimens were examined from the following herbaria (acronyms follow Holmgren et al. 1990): BRIT, C, CIIDIR, CM, E, GH, K, M, MEXU, MICH, MO, NU, NY, P, PH, PRE, RSA, SMU, TAES, TEX, US, WIS, Z, and ZT. Additional specimens were requested from CGE, LINN, and USJ, but loans were not available, or a response not received.

Populations

Field work in 2002 resulted in the discovery of *Eleocharis mutata* in Texas, and collections were made of a population comprising 10 reproductively mature specimens (Rosen & Jones 2004). Additional artificial populations of *E. mutata* were established from the herbarium specimens available for study. Ninety mature specimens displaying the full range of morphological variation observed that were complete for all characters measured and originating from throughout the known geographical distribution of *E*. *mutata* were selected. These included type specimens for both *E*. *mutata* and *E*. *scariosa*.

Multivariate Analysis

Initially, morphological characters were gleaned from the literature dealing with studies investigating closely related species or infraspecific variation of *Eleocharis*. Subsequently, examination of *E*. *mutata* in the field, along with study of herbarium specimens, including type specimens, resulted in selecting 17 morphological characters for evaluation (Table 2). For each specimen, a spikelet with fully developed achenes was selected. For measurement of floral characters, an achene and its subtending scale were selected from near the base of the spikelet.

A total of 100 operational taxonomic units (OTUs) of *Eleocharis mutata* were numerically analyzed representing its full geographic distribution: United States of America (10 OTUs); Mexico (10 OTUs); Central America (10 OTUs); South America (30 OTUs); Caribbean Basin (30 OTUs); and Africa (10 OTUs). Each specimen measured was complete for all characters so that the data matrix contained no missing values. Micromorphological characters were measured with an Olympus™ SZ-40 dissecting microscope equipped with an ocular micrometer. When necessary, particularly when examining floral scales, dissection was aided with the use of Pohl's solution (Pohl 1965).

Table 2. Initial 17 characters used to evaluate worldwide morphological variation of *Eleocharis mutata*. All characters are continuous quantitative (CQ) except for LONROW which is discrete (D).

Symbol	**Character**	**Type**	**Unit**
ACHNBL	achene body length (from base to region of constriction at annulus)	CQ	mm
ACHNBLW	ratio of achene body length to width (achene shape)	CQ	ratio
ACHNMAX	ratio of achene body length to distance from achene base to widest point	CQ	ratio
ACHNSCAL	ratio of achene length to floral scale length	CQ	ratio
ACHNW	achene body width (at widest point)	CQ	mm
ANULACHW	ratio of annulus width to achene width	CQ	ratio
ANULH	height of annulus	CQ	mm
ANULHW	ratio of annulus height to annulus width (annulus shape)	CQ	ratio
LONBRSTL	length of longest perianth bristle	CQ	mm
LONROW	longitudinal rows of cells on achene face	D	number
SCALEL	floral scale length	CQ	mm
SCALELW	ratio of floral scale length to width (floral scale shape)	CQ	ratio
SCALEW	floral scale width	CQ	mm
TBCXL	tubercle complex length	CQ	mm
TBCXLW	ratio of tubercle complex length to width (tubercle complex shape)	CQ	ratio
TBCXW	tubercle complex width (= annulus width)	CQ	mm
TBRCL	tubercle length	CQ	mm

The raw morphometric data were standardized and analyzed by PCA using NTSYSpc 2.11Q (Rohlf 2000). The principal components were generated using a correlation matrix. The initial character set was scored using PCA, and characters found to be highly intercorrelated or with low loadings were removed and the analysis re-run. For the final analysis, a scree plot was generated to determine how many principal components to extract (Rencher 1998). Scatter plots of the first three principal components were generated in an effort to detect groups which might represent infraspecific taxa in *E. mutata*.

PCA is an ordination procedure that reduces the variance-covariance structure of a set of *p* variables to a few linear combinations (principal components) of these variables and, as such, is a dimension or data reducing technique (Rencher 1998; Johnson & Wichern 2002). The purpose of data reduction is to remove redundant variables from the data matrix, replacing them with a smaller number of uncorrelated variables. Principal components analysis finds a linear combination of variables that accounts for as much variation in the original variables as possible, followed by another component that accounts for as much of the remaining variation as possible and is uncorrelated with the first principal component, continuing until there are as many components as original variables. However, a few principal components will account for most of the variation, and these components can be used to replace the original variables. The principal components comprise a new set of orthogonal axes representing the directions with maximum variability and yield a parsimonious description of the covariance structure provided the variables are not highly intercorrelated (Rencher 1998; Johnson & Wichern 2002). When the coefficients of the individual multivariate observations of the first two or three components are plotted, they can be examined more easily than can all the numerous possible combinations of the variables.

An additional classification was attempted by producing a dendrogram of the entire data matrix using NTSYSpc 2.11Q (Rohlf 2000). Averages for each character were standardized using the STAND module. Next, a similarity or dissimilarity matrix was produced that measured the degree of dissimilarity between all pairs of OTUs of the standardized data matrix using the SIMINT module. The SAHN module was then used to perform a UPGMA cluster analysis. In order to see how well a cluster analysis represented the distance matrix, the COPH module was used to transform the tree matrix to a matrix of ultrametric distances (a matrix of distances implied by the cluster analysis).

RESULTS

The first three principal components explain 74% of the total variance (37.9%, 21.8%, and 14.3% for PC1, PC2, and PC3, respectively; Table 3). PCA axis 1 is most influenced by high positive loadings of tubercle complex length, the shape of the tubercle complex (tubercle complex length/annulus width), and tubercle length; PCA axis 2 is most highly influenced by high negative loadings of tubercle complex width (Fig. 11; Table 3). A scatter plot of the first two principal components (Fig. 12), and a three-dimensional scatter plot of the first three principal components (Fig. 13) show no discernable infraspecific variation based on geographic distribution. All geographic populations overlap for the characters evaluated, and there is no indication of any geographical group forming a distinct cluster. For the UPGMA cluster analysis, the matrix correlation (= cophenetic correlation) suggested a fit of r = 0.7, though the dendrogram did not clearly separate any clusters based on geographic distribution as all OTUs are intermixed on the tree (Fig. 14).

Table 3. Results of PCA of worldwide variability of *Eleocharis mutata* for 10 variables of 100 OTUs.

	PC1	**PC2**	**PC3**
Eigenvalues	3.79	2.18	1.43
Component Loadings			
ACHNBLW	0.01	0.55	0.67
ACHNMAX	-0.01	0.03	-0.67
TBRCL	0.86	-0.40	-0.12
TBCXL	0.92	-0.27	-0.03
TBCXW	0.17	-0.86	0.22
TBCXLW	0.92	0.09	-0.06
ANULHW	0.48	0.65	0.19
ANULACHW	-0.14	-0.63	0.61
LONBRSTL	0.77	0.16	-0.02
SCALEL	0.69	0.21	0.25
Percent of total variance explained	37.9	21.8	14.3

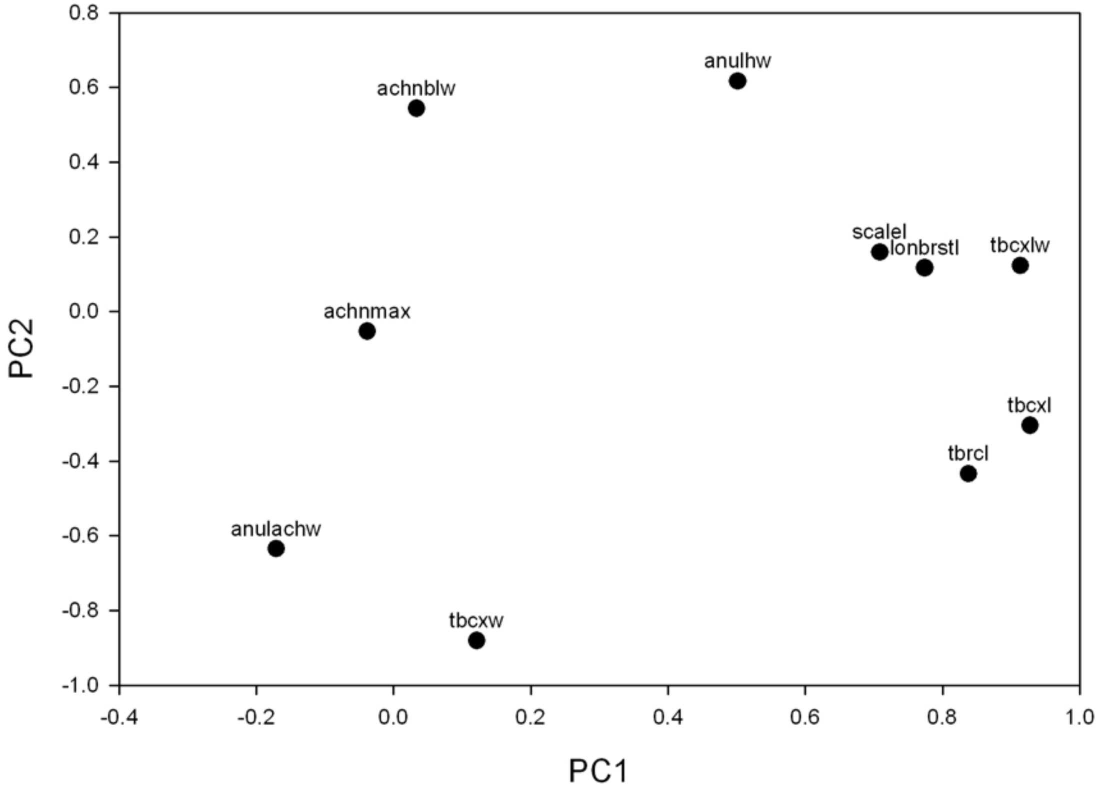


Fig. 11. PCA character loadings for analysis of *Eleocharis mutata*. Character abbreviations follow those from Table 2.

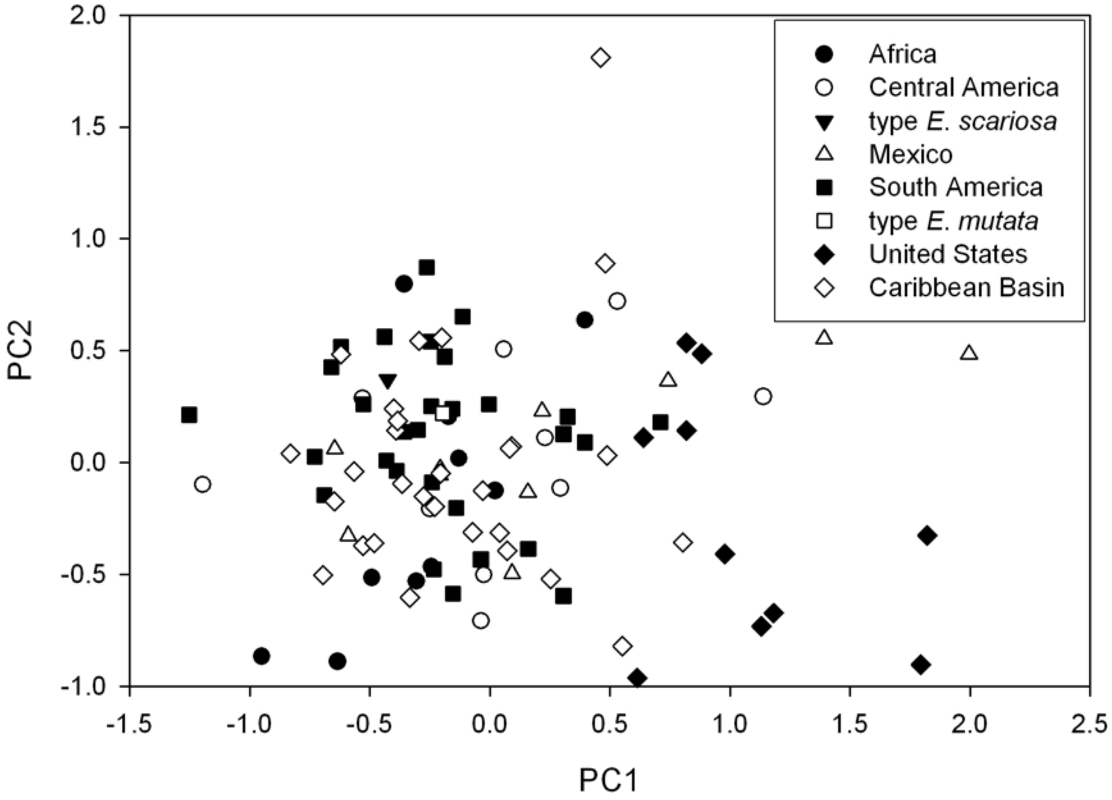


Fig. 12. Two-dimensional scatter plot of PCA ordination (PC1 vs. PC2) of worldwide populations of *Eleocharis mutata*.

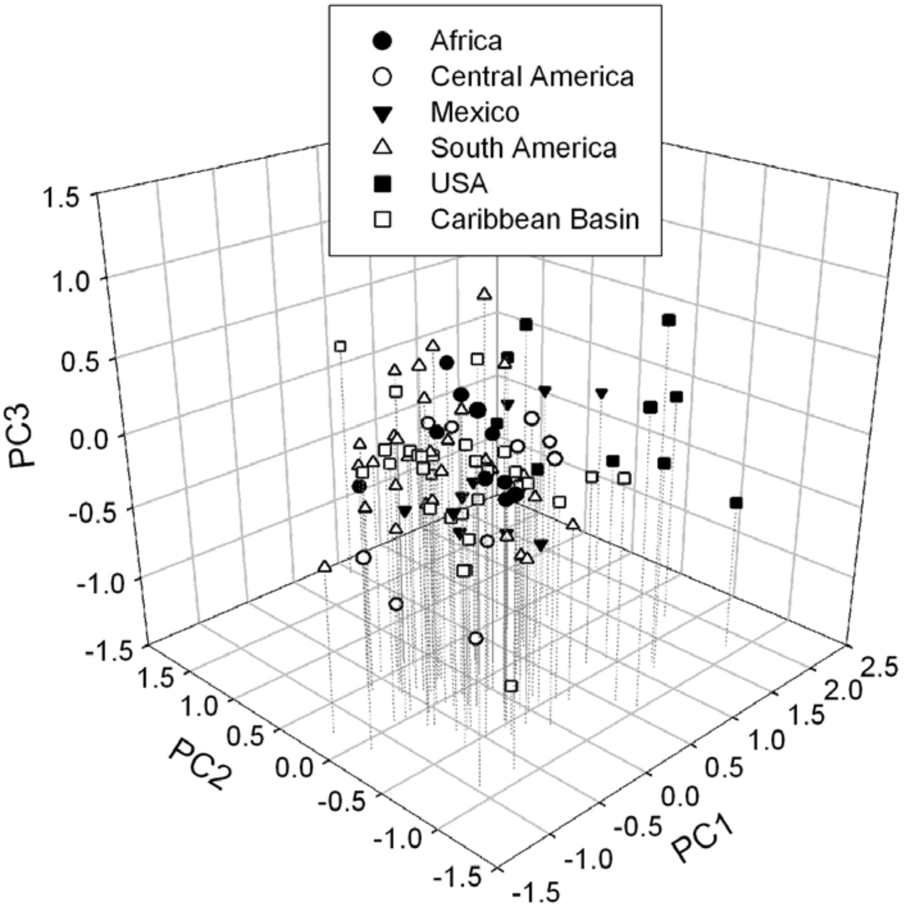


Fig. 13. Three-dimensional scatter plot of PCA ordination of worldwide populations of *Eleocharis mutata*.

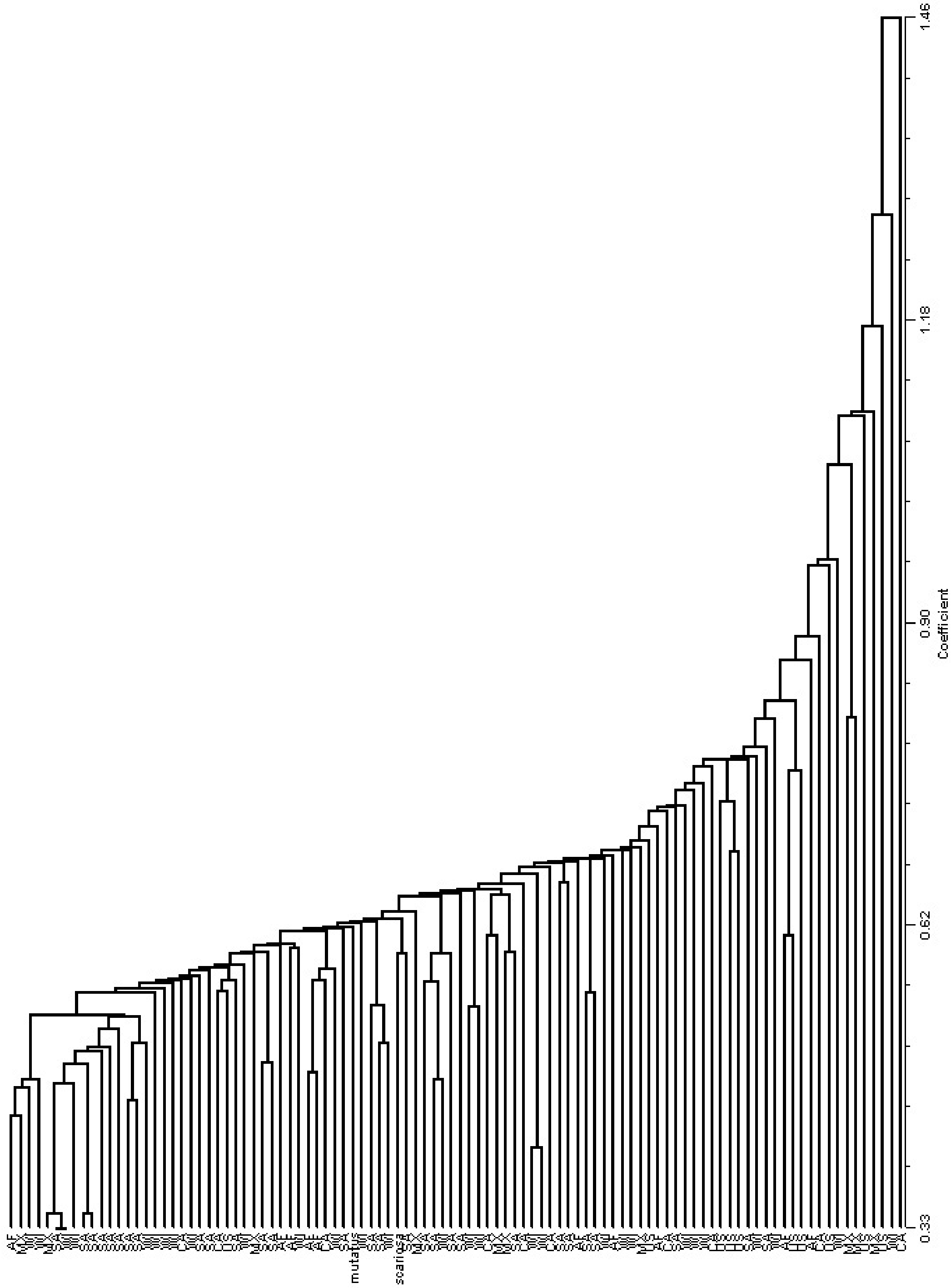


Fig. 14. UPGMA dendrogram based on 17 morphological characters. Geographic codes are: AF = Africa, CA = Central America, MX = Mexico, SA = South America, US = U.S.A., and W I= Caribbean Basin. Types are *Scirpus mutatus* (mutatus) and *Eleocharis scariosa* (scariosa).

DISCUSSION

Clear morphological separation among widely ranging geographic populations of *Eleocharis mutata* could not be found. Variability of the tubercle in *E*. *mutata* was first indicated in the literature by line drawings in Fernald (1925, plate 149, 11-14). After review of over 450 specimens of *E*. *mutata* from throughout its distribution, notable variation was observed in the shape and texture of the tubercle complex (comprised by the tubercle and annulus), sometimes in achenes from the same accession. The PCA indicates that this variation is well represented throughout the distribution of *E*. *mutata* and is scattered around the type specimens (Fig. 12). The dorsoventrally compressed tubercles can be triangular and distinct or withered and appearing to merge with or be shouldered by the annulus. Since the tubercle represents the dried remnant of the style base, some variation within a species could be expected by the stage of maturity at which a specimen is collected and the conditions (relative humidity, temperature, and duration) under which the specimen is preserved.

Figure 12 illustrates Old World (African) specimens were less variable for the characters evaluated than those of the New World. Individual points of *Eleocharis mutata* from Africa were almost completely imbedded within those of the New World (Fig. 12).

Collections of African *E*. *mutata* are poorly represented in large herbaria worldwide, and few specimens were available for study (Appendix I), which suggests it is rare or possibly poorly understood and under-collected there. Moreover, the recent report of *E*. *mutata* new to southern Africa indicates it might be recently introduced there (Browning et al. 1995).

CONCLUSION

This morphometric numerical study supports the conclusion that *Eleocharis mutata* is represented by a single taxon throughout its distribution. Morphological variability of achene characters associated with the tubercle was observed, predominantly tubercle complex length and shape as influenced by tubercle length and tubercle complex width. This particular morphological variability is thought to be a relict of factors associated with preservation of herbarium specimens, and although not presently accounted for in species descriptions, it should be. Blake (1939) observed that “the style-base in its general characteristics is relatively constant, often through whole groups, although in detail it may vary widely within a species”. Larson & Catling (1996, Fig. 3) found considerable morphological variability in the achenes of *E*. *ovata* and *E*. *obtusa*. Despite the variability observed in *E*. *mutata*, it can be consistently and confidently identified by careful examination using the presence of the following suite of characters: (1) triquetrous to trigonous or less commonly obscurely 3-angled (terete) culms; (2) finely many-veined cartilaginous floral scales abaxially and adaxially red-maculate, frequently with a dark band near apex; (3-)6-8 course, retrorsely spinulose perianth bristles mostly exceeding the achene summit; and, (4) longitudinally striate, biconvex, more or less obpyriform or obovate or sometimes broadly elliptic achenes, their apex constricted to about 0.6 times their width, broadening into a hard annulus of the same texture and color as the achene.

Eleocharis mutata is apparently rare, of limited distribution, and displays less variability in Africa, and is proposed herewith to be introduced there from the New World, possibly by several events of long range dispersal. This is consistent with the founder principal, which states less morphological variation might be expected in a founder population than the parent population from which it originated (Jones & Luchsinger 1986). This study has considerably expanded Svenson's previously published distribution of *E*. *mutata*. Its occurrence throughout the Atlantic-Caribbean-Pacific archipelagos of the New World suggests it is readily spread by trans-oceanic dispersal. The conclusion by Browning et al. (1997) that *E*. *mutata* is "nowhere common or extensive" is not supported by this study (see Appendix I).

Figure 15 depicts *E. mutata* as being a widely distributed, sub-pantropical species in coastal habitats from Southeast Texas, Mexico, Central America, tropical South America, the Caribbean Basin, and tropical Africa. Ecologically, it can be dominant, and form vast, pure stands in coastal wetlands (Palma-Silva et al. 2000; Rosen, pers. obs. 2002-2006).

This and the previous study also do not support the interpretation by Browning et al. (1997) that such a widespread and ecologically important species in the New World could be the resulting hybrid of two apparently Old World species. Although hybrids have been documented in *Eleocharis*, they usually have high levels of fruit abortion, and display characteristics intermediate between the putative parents (Catling and Hay 1993; Catling 1994). Mature specimens of *Eleocharis mutata* examined typically had a high percentage of flowers ripening into well developed achenes.

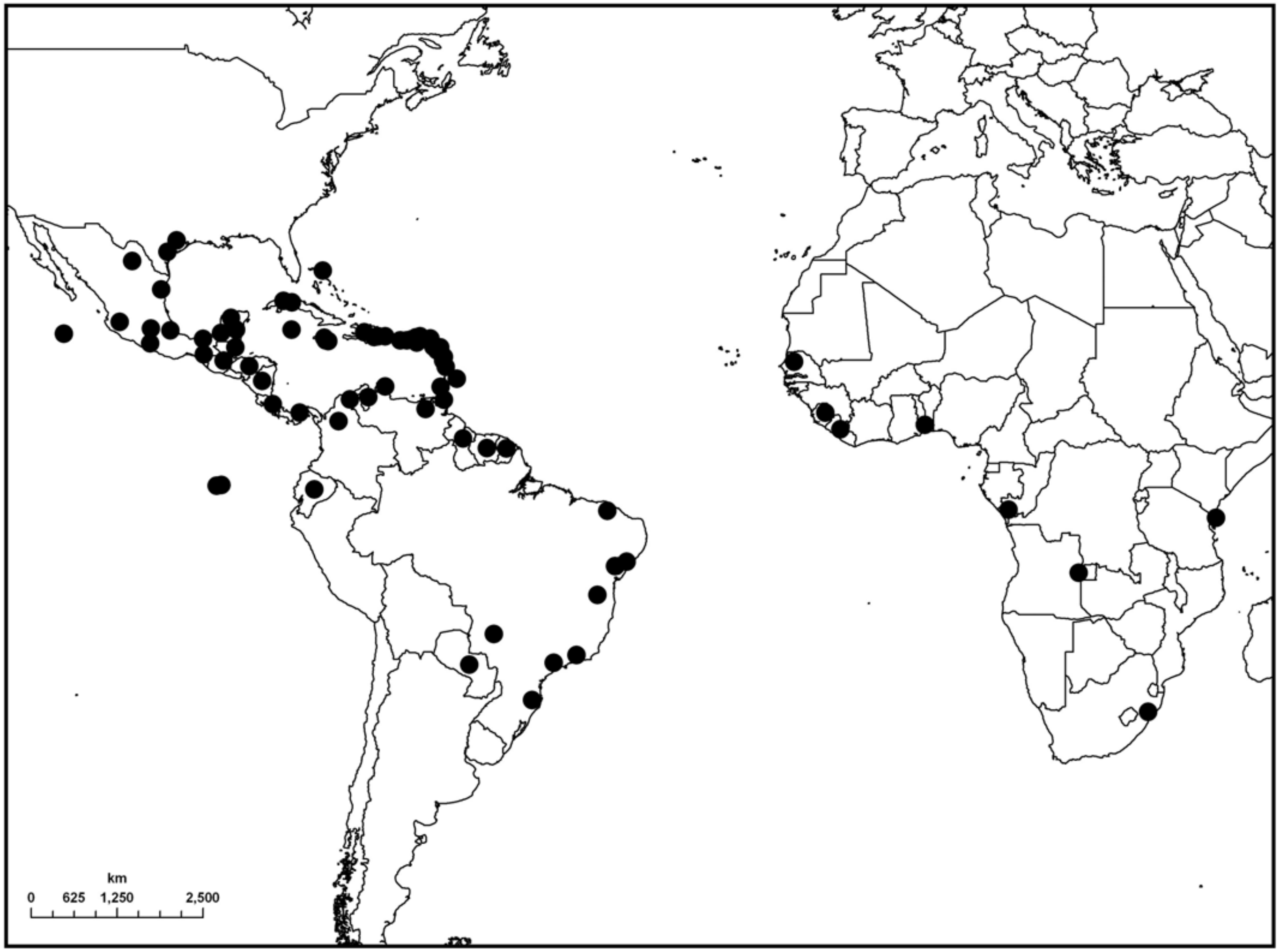


Fig. 15. Geographic distribution of *Eleocharis mutata*. Each dot represents the general geographic location of one or more specimens.

With the exception of triangular culms, *E*. *mutata* shares few other vegetative characters with *E*. *acutangula*. As described in Chapter II, achene macro- and micromorphology are markedly different between *E*. *acutangula* and *E*. *mutata*. With *E*. *dulcis*, *E*. *mutata* shares no salient characters other than those general characters expected for subg. *Limnochloa*.

CHAPTER IV

MORPHOMETRIC NUMERICAL STUDY OF THE TAXONOMIC RELATIONSHIP OF *ELEOCHARIS MUTATA* AND *ELEOCHARIS SPIRALIS*

INTRODUCTION

Eleocharis mutata and *E*. *spiralis* are members of subg. *Limnochloa* notable for their prevalence in coastal, usually brackish or saline wetlands of the Old and New World tropics (Blake 1939; Hooper 1972; Kern 1974; Haines & Lye 1983; Gonzáles-Elizondo 1994; Simpson & Koyama 1998). Rottböll described *E*. *spiralis* based on specimens from Malabaria (India) and indicated it resembled *E*. *mutata*. Böckeler (1870) referred *E*. *mutata* to *E*. *spiralis*, whereas Clarke (1900) regarded *E*. *mutata* and *E*. *spiralis* to be quite different. Svenson (1929) considered *E*. *spiralis* to be closely related to *E*. *mutata*, differing from it in its firmer, sharply truncate scales; shorter and thicker spikelets; and achene texture, ornamentation (smoother and finer in *E*. *spiralis*), and color. Svenson (1929) contrasted *E*. *spiralis* with *E. cellulosa* on the basis of elongated, linear achene cells, less spongy beak, toothed perianth bristles, and truncate scales in *E*. *spiralis*. Furthermore, Svenson (1929) suggested that *E*. *mutata*, *E*. *cellulosa*, and *E*. *spiralis* formed a group of closely related species, all possessing spongy textured achenes and characteristic beaks. Svenson’s reference to a beak, in regards to these three species, refers to the annular thickening that surmounts the achene apex. Whereas the term beak most appropriately describes the stout, spongy, tapered thickening of *E*. *cellulosa*, in *E*. *mutata* the annulus is typically oblong, usually distinct, and merges abruptly into a dorsoventrally compressed tubercle. In *E*. *spiralis*, the annulus is narrowly oblong (indistinct in some specimens) merging abruptly into a dorsoventrally compressed tubercle, very similar in general aspect to *E*. *mutata*. However, in some specimens of *E*. *spiralis* the annulus can be prolonged and tapered, merging into a short conical tubercle, very similar to *E*. *cellulosa*.

Examination of numerous herbarium specimens reveals both conditions can be observed in different achenes of the same accession (e.g., *Koyama 14014*, NY; *Koyama 14060*, GH). Some specimens of *E*. *spiralis* have truncate scales, giving the spikelets a strongly compact appearance. However, numerous specimens referable to *E*. *spiralis* in regard to characters of the achene and perianth bristle texture had scales with a broadly rounded apex, indistinguishable from *E*. *mutata*. Both taxa also share culm cross sectional shape that can range from trigonous to obscurely three angled.

The taxonomic relationship of *Eleocharis spiralis* and *E*. *mutata* has never been satisfactorily investigated and resolved. That *E*. *mutata* and *E*. *spiralis* are taxonomically distinct is apparent, but at what rank is in need of systematic investigation.

Additionally, the geographic distribution of both species needs to be studied, updated, and mapped. Recent floristic treatments have reported the two species as sympatric in South America (Koyama 1985; Simpson & Koyama 1998). Kern (1974) suggested that *E*. *spiralis* might be better treated as a subspecies of *E*. *mutata*. Since no critical comparison of the two taxa based upon specimens from throughout their respective ranges has ever been published, this study sought to examine the taxonomic relationship of *E*. *spiralis*, its synonyms *E*. *compacta* and *E*. *austro-caledonica*, and *E*. *mutata* by morphometric numerical analysis, and to map their geographic distribution.

MATERIALS AND METHODS

Specimen Selection

Specimens of *Eleocharis mutata* and *E*. *spiralis* from the following herbaria were examined for this study: BHM, BRI, BRIT, C, CM, CIIDIR, E, GH, K, LIV, M, MEXU, MICH, MO, NU, NY, P, PH, PRE, SMU, TAES, US, WIS, Z, and ZT. Although specimens of *E*. *spiralis* and its synonyms were requested from over 30 large domestic and foreign herbaria, only 78 were received for study, and fewer were suitable for measurement. Additional type specimens for the various synonyms were sought as they came to light following an extensive literature review and correspondences with cyperologists worldwide. Forty-five mature specimens that were complete for all selected characters and that originated from throughout the known geographical distribution of *E*. *spiralis* were selected (including two type specimens). For this study, a subset of 45 multivariate observations for *E*. *mutata* were randomly selected from a data matrix used in the previous study.

Univariate and Multivariate Analysis

Examination of approximately 530 herbarium specimens, including type specimens, resulted in selecting 21 morphological characters for evaluation (Table 4). For each specimen, a spikelet with fully developed achenes was selected. For measurement of floral characters, an achene and its subtending scale were selected from near the base of the spikelet. Each specimen measured was complete for all characters so that the data matrix contained no missing values. In order to elucidate the taxonomic relationship of *Eleocharis mutata* and *E*. *spiralis*, a data matrix of multivariate observations for 90 OTUs (45 of each taxon classified *a priori*) were explored using two multivariate statistical analyses. The discriminant analysis (DA) procedure in Statistical Package for Social Sciences 11.5 (SPSS 2003) using a within-groups covariance matrix was used to build a classification model by determining the order of reliability of the initial morphological characters selected to separate *E*. *spiralis* and *E*. *mutata* (Table 4). Discriminant analysis attempts to find linear combinations of those variables that best separate groups of cases. For two groups, DA generates a discriminant function based on linear combinations of the predictor variables (= Fisher linear discriminant analysis) that provide the best discrimination between the groups. The function is generated from the sample of cases for which group membership is known; the function can then be applied to new cases with measurements for the predictor variables but unknown group membership.

Table 4. Initial characters used in DA to evaluate taxonomic relationship of *Eleocharis mutata* and *E*. *spiralis*. Characters are continuous quantitative (CQ), discrete (D), or qualitative (QL). [1]CELLS was not used in DA.

Symbol	**Character**	**Type**	**Unit**
ACHNBL	achene body length (from base to region of constriction at annulus)	CQ	mm
ACHNBLW	ratio of achene body length to width (achene shape)	CQ	ratio
ACHNL	achene length (including tubercle complex)	CQ	ratio
ACHNMAX	ratio of achene body length to distance from achene base to widest point	CQ	ratio
ACHNSCAL	ratio of achene length to floral scale length	CQ	ratio
ACHNW	achene body width (at widest point)	CQ	mm
ANULACHW	ratio of annulus width to achene width	CQ	ratio
ANULH	height of annulus	CQ	mm
ANULHW	ratio of annulus height to annulus width (annulus shape)	CQ	ratio
[1]CELLS	shape of achene cells at mid body (0= transversely oblong, 1 = transversely linear)	QL	-
LONBRSTL	length of longest perianth bristle	CQ	mm
LONGROWS	longitudinal rows of cells on achene face	D	number
SCALEL	floral scale length	CQ	mm
SCALELW	ratio of floral scale length to width (floral scale shape)	CQ	ratio
SCALEW	floral scale width	CQ	mm
SPIKELL	spikelet length	CQ	mm
SPIKELW	spikelet width	CQ	mm
TBCXL	tubercle complex length	CQ	mm
TBCXLW	ratio of tubercle complex length to width (tubercle complex shape)	CQ	ratio
TBCXW	tubercle complex width (= annulus width)	CQ	mm
TBRCL	tubercle length	CQ	mm

For the DA analysis in SPSS, Fisher's linear discriminant function was used to assign cases to groups. The DA procedure in SPSS also provides, for each variable, means, standard deviations, Wilks' lambda, and one-way analysis of variance (ANOVA) between group means before the model is created. Decisions about which characters to carry forward in subsequent analysis were made by examining the standardized canonical discriminant function coefficients and a pooled within-groups correlation structure matrix.

A suite of characters found to best classify *Eleocharis spiralis* and *E*. *mutata* by DA, and an additional qualitative variable, were then used to extract principal components using NTSYSpc 2.11Q (Rohlf 2000). The principal components were generated using a correlation matrix. Scatter plots of the first three principal components were generated in an effort to evaluate the taxonomic distance of *E*. *spiralis* and *E*. *mutata*.

RESULTS

Discriminant and Univariate Analysis

The DA resulted in a discriminant function that classified specimens of *Eleocharis spiralis* and *E*. *mutata* 97.8% of the time. Only a small proportion of the total variance (Wilk’s Lambda = 0.192) in the dicriminant scores was not explained by differences among groups. The most useful variables for discriminating between groups were LONBRSTL, LONGROWS, SPIKELL, TBCXW, TBCXLW, ACHNW, ACHNSCAL, SCALEL, TBXACHW, and ACHNBLW. The one-way analysis of variance (ANOVA) separated the two groups for the same suite of characters (Table 5). Although there is considerable variability in the characters measured for both groups and overlap of the ranges for all variables, when the characters ranked high by DA and ANOVA are coupled with several qualitative variables to be discussed later, the two taxa can be readily separated.

Principal Components Analysis

The first three principal components explain 66.2% of the total variance (37%, 17.5%, and 11.7% for PC1, PC2, and PC3 respectively; Table 6). PCA axis 1 is most highly influenced by negative loadings for achene cell shape and positive loadings for annulus width, length of longest perianth bristle, and achene width; PCA axis 2 is most highly influenced by negative loadings for scale length and positive loadings for the ratio of annulus width to achene width (Fig. 16). A scatter plot of the first two and first and third principal components

(Fig. 17; Fig. 18) and a three-dimensional scatter plot of the first three principal components (Fig. 19) show a distinct separation of *Eleocharis spiralis* and *E*. *mutata*.

Phytogeography

Figure 20 depicts *Eleocharis mutata* as being a widely distributed, sub-pantropical species in coastal habitats from Southeast Texas, Mexico, Central America, tropical South America, the Caribbean Basin, and tropical Africa. During examination of over 450 herbarium specimens, numerous specimens of *E*. *mutata* misidentified as *E*. *acutangula*, *E*. *cellulosa*, *E*. *fistulosa*, *E*. *interstincta*, and *E. spiralis* were encountered. Specimens of *E*. *mutata* from Puerto Rico (*Sintenis 4942*; M, Z, ZT) annotated by Boeckeler as *E. spiralis* appear to form the basis for which *E. spiralis* is reported from the New World.

Eleocharis spiralis is rare throughout the Indo-Malayan tropics with records from India, Sri Lanka, Thailand, Vietnam, China, The Philippines, Malaysia, Papua-New Guinea, and New Caledonia, but apparently is more commonly collected in Queensland and Northern Territories of Australia. No authentic material of *E*. *spiralis* from Madagascar was observed, however, Svenson (1939) cited it as introduced there (*Perrier de la Bathie 2498*, B, presumably now destroyed). This specimen was not examined, but, since Svenson's annotations are highly reliable, the report is considered authentic and has been mapped.

Table 5. Means and ranges (mean ± 1 standard deviation) for quantitative morphological characters of *Eleocharis mutata* and *E*. *spiralis*. Characters represent those found significantly different ($P \leq 0.05$) by one-way analysis of variance (ANOVA). Character abbreviations and units of measure are listed in Table 4.

Character	***E. mutata***	***E. spiralis***	**ANOVA (*F*)**
ACHNW	1.23 1.12-1.34	1.16 1.04-1.28	8.3
ACHNBLW	1.20 1.1-2.2	1.27 1.06-1.48	4.0
TBCXW	0.72 0.63-0.81	0.66 0.58-0.74	14.0
TBCXLW	0.78 0.6-0.96	0.90 0.73-1.07	11.5
TBCXACHW	0.59 0.53-0.65	0.56 0.52-0.6	5.3
SCALEL	3.56 3.11-4.01	3.31 2.79-3.83	5.8
ACHNSCAL	0.57 0.51-0.63	0.63 0.5-0.76	7.0
SPIKELL	31.6 23.76-39.6	25.7 18.73-32.63	14.3
LONBRSTL	2.33 1.87-2.79	1.54 1.28-1.8	101.1
LONGROWS	21 18-24	17 15-19	48

Table 6. Results of PCA of *Eleocharis mutata* and *E*. *spiralis* for 11 variables of 95 OTUs.

	PC1	**PC2**	**PC3**
Eigenvalues	4.07	1.93	1.28
Component loadings			
ACHNW	0.70	0.13	0.08
ACHNBLW	-0.55	-0.21	-0.59
TBCXW	0.76	0.50	-0.03
TBCXLW	-0.38	-0.51	-0.34
TBXACHW	0.35	0.61	-0.14
SCALEL	0.60	-0.61	0.12
ACHNSCAL	-0.54	0.43	-0.57
SPIKELL	0.54	-0.53	-0.02
LONBRSTL	0.71	-0.33	-0.46
LONGROWS	0.69	0.19	-0.29
CELLS	-0.73	0.01	0.39
Percent of total variance explained	37	17.5	11.7

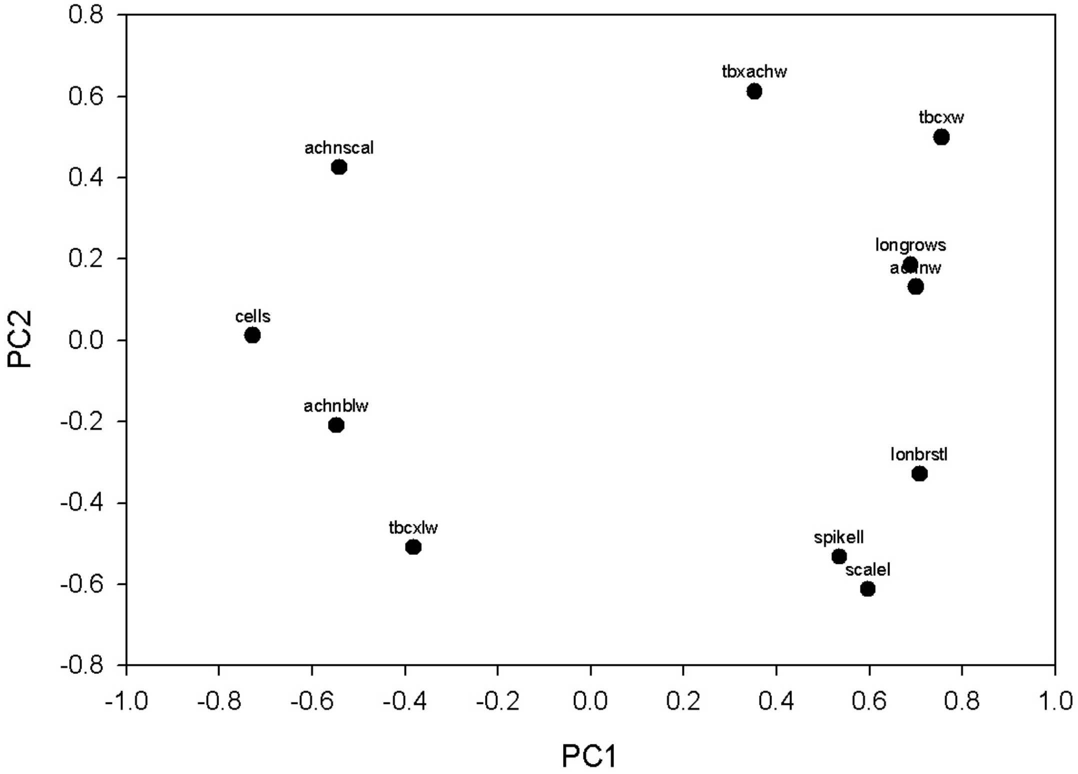


Fig. 16. PCA character loadings for analysis of *Eleocharis mutata* and *E. spiralis*. Character abbreviations follow those from Table 4.

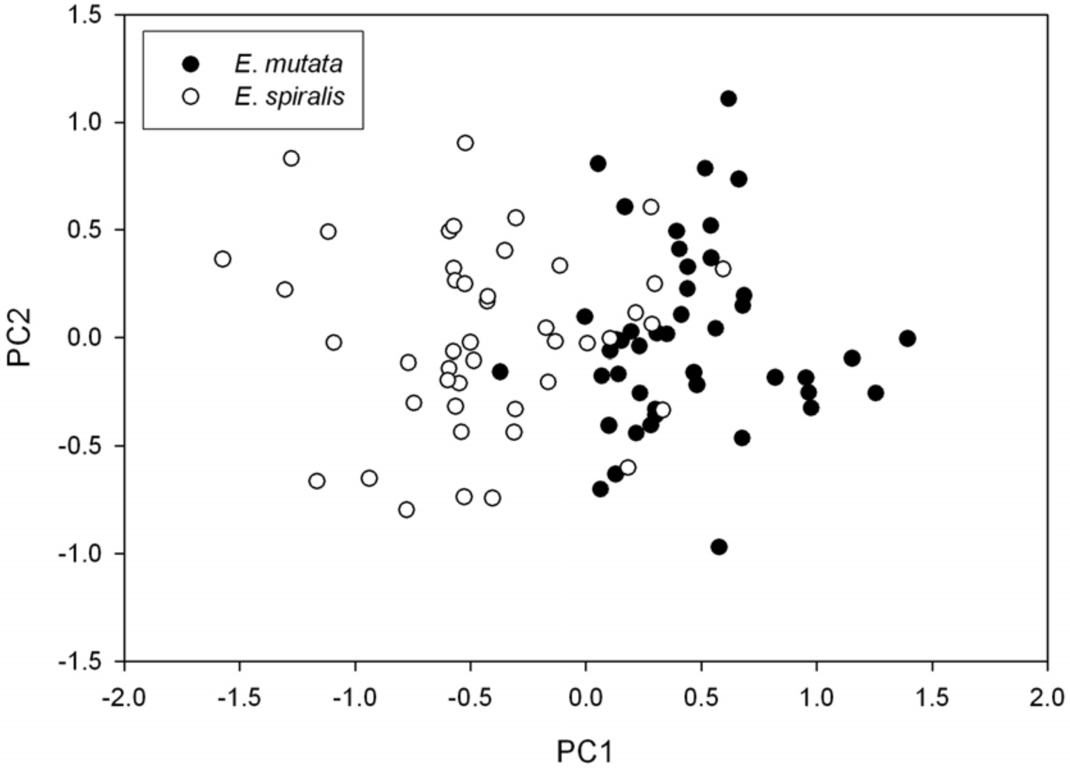


Fig. 17. Two-dimensional scatter plot of PCA ordination (PC1 vs. PC2) of *Eleocharis mutata* and *E. spiralis*.

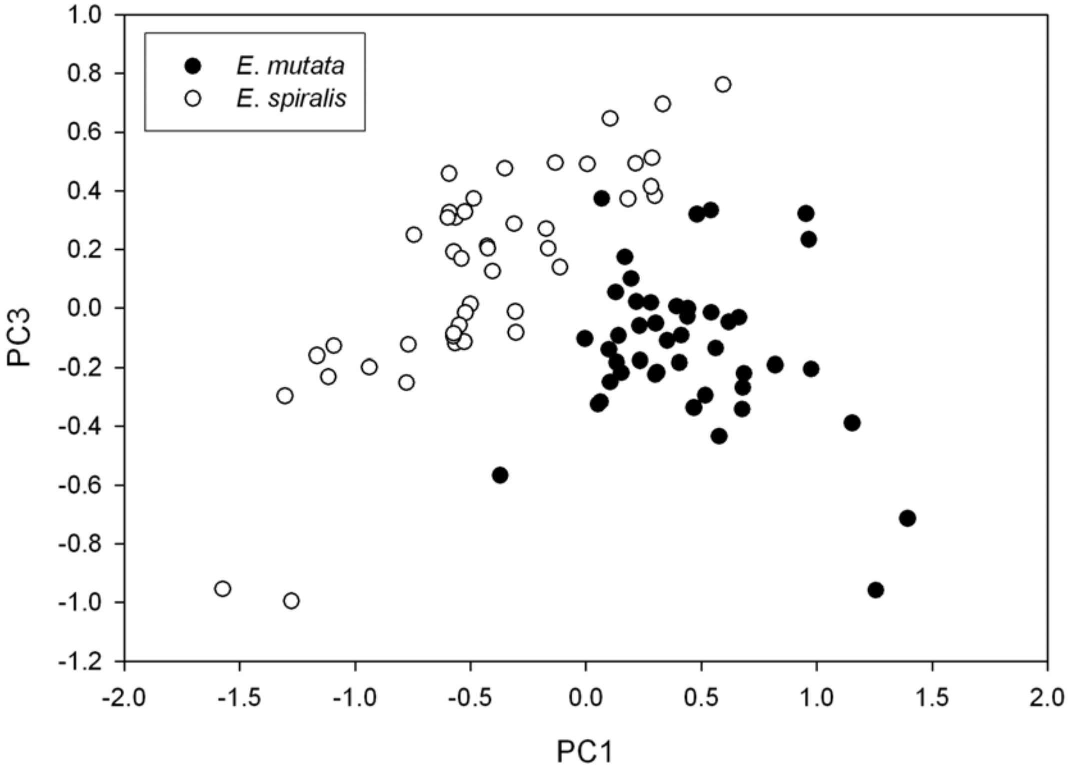


Fig. 18. Two-dimensional scatter plot of PCA ordination (PC1 vs. PC3) of *Eleocharis mutata* and *E. spiralis*.

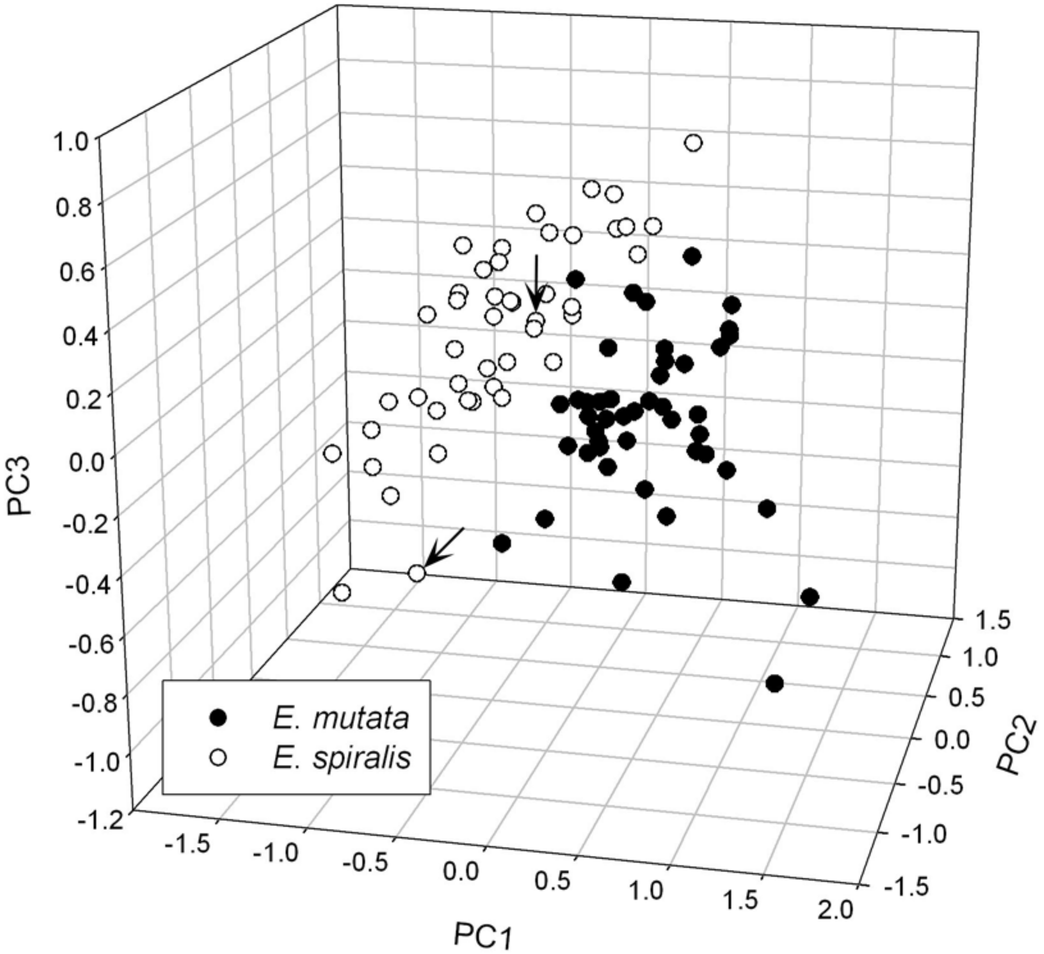


Fig. 19. Three-dimensional scatter plot of PCA ordination of *Eleocharis mutata* and *E*. *spiralis*. Arrows indicate types of *E*. *spiralis*.

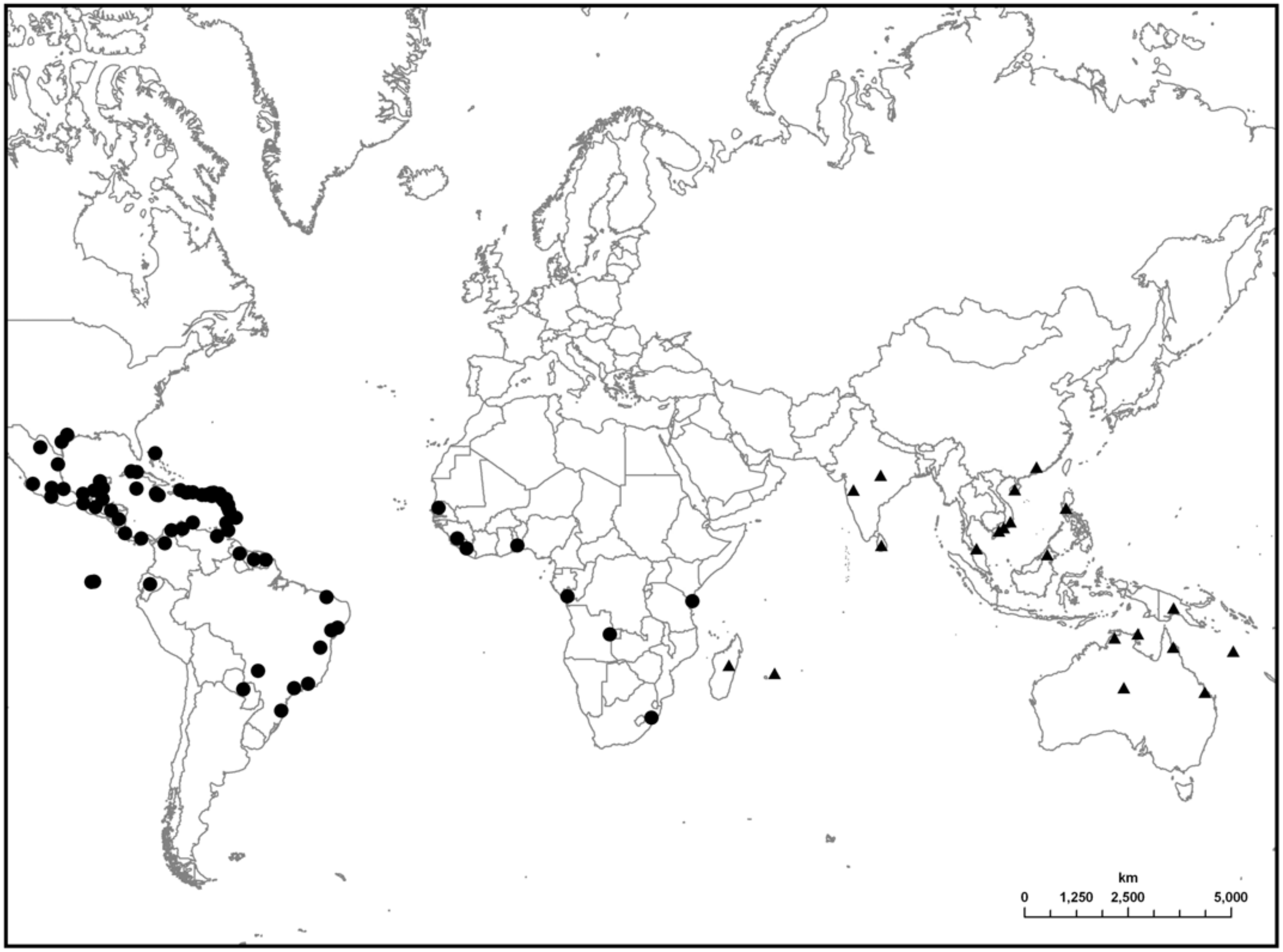


Fig. 20. Geographic distribution of *E*leocharis *mutata* (●) and *E*. *spiralis* (▲). Each dot represents the general geographic location of one or more specimens.

DISCUSSION AND CONCLUSION

The results of the DA, PCA, and phytogeography support recognizing *Eleocharis mutata* and *E*. *spiralis* as taxonomically distinct. Type specimens of *E*. *compacta* (*Brown 5934*, K-2 sheets) and *E*. *austro-caledonica* (*Vieillard 1453*, BM) were not suitable for measurement, but, upon critical examination, it is clear that they were referable to *E*. *spiralis*. Type specimens of *E*. *austro-caledonica* at P and CGE were available only as poor resolution photographs. On examination of the photographs the culms are conspicuously septate and spikelet characteristics do not agree with *E*. *spiralis*. However, Svenson (1939) examined a type specimen of *E*. *austro-caledonica* (K, apparently now lost), and placed it in synonymy under *E*. *spiralis*. Apparently the “types” of *E*. *austro-caledonica* comprise a mixed collection.

This study reveals that *E*. *mutata* and *E*. *spiralis* are genetically isolated through an allopatric distribution, and all specimens were fully differentiated and readily distinguished by a suite of diagnostic, genetically determined characters. For these reasons, the two taxa remain recognized herewith at the rank of species. Through careful and critical examination, specimens of *E*. *mutata* and *E*. *spiralis* can be separated by the quantitative characters determined in the univariate and multivariate analysis (ACHNW-LONGROWS, Table 5). At high magnification (40×) several qualitative characters will readily distinguish the two taxa as follows: *Eleocharis mutata* achenes have transversely oblong rectangular cells with prominent longitudinal interstitial ridges and coarse-retrorsely spinulose perianth bristles; whereas, *E*. *spiralis* has transversely linear cells with inconspicuous longitudinal interstitial ridges, and fine, irregularly spinulose to smooth perianth bristles.

Eleocharis spiralis is reported in recent literature as occurring in the New World (Koyama 1985; Simpson & Koyama 1998). This may be attributable to Böckeler's and others misapplication of *E*. *spiralis* to South American specimens of *E*. *mutata*. Because no authentic specimens of *E*. *spiralis* from the New World were found, it should be deleted from the New World flora. The opportunity for study of *E*. *spiralis* in the field was not feasible, but the literature and specimen label data suggests it and *E*. *mutata* may be ecological equivalents in their respective ranges, forming large colonies in brackish or saline habitats (Kern 1974; Cowie et al. 2000; Palma-Silva et al. 2000).

CHAPTER V

MORPHOMETRIC NUMERICAL STUDY OF POTENTIAL INFRASPECIFIC SEGREGATES OF *ELEOCHARIS CELLULOSA*

INTRODUCTION

The distribution of *Eleocharis cellulosa* is restricted to the coastal plain of the southeast United States, Caribbean, Mexico, Central America, and northern South America (Venezuela). It is an ecologically important species that can form dense, pure stands in costal wetland systems. It has been suggested that the variation in this species throughout its range is in need of investigation (González-Elizondo, personal communication). During field work in southern Texas in 2004, plants of *E*. *cellulosa* growing in deep-water of coastal wetlands were observed to have tall, spongy, nearly trigonous culms, whereas plants growing in desiccated situations had short, stiff, more or less terete culms. Recent research has indicated that culm height, width, and leaf sheath length in *E*. *cellulosa* respond to water depth manipulation (Edwards et al. 2003; Baksh and Richards 2006). Suffice it to say that variation in vegetative characters among populations of *E*. *cellulosa* is little basis for recognition of infraspecific taxa. Svenson (1939) reported reviewing specimens of *E*. *cellulosa* from Puerto Rico with strongly barbed bristles. Reports of *E*. *cellulosa* with trigonous culms and spinulose bristles have been described in recent treatments of the species in Mesoamerica and North America (González-Elizondo 1994; 2002).

The occurrence of spinulose bristles in a species known to have typically smooth bristles could be taxonomically important. Svenson (1929) noted that bristle texture was very constant within a species, and may be one of the most valuable means for identification. The variability of perianth bristle texture previously reported for *Eleocharis cellulosa* is the focus of the research reported here. This study also compares material from throughout the range of the species with type specimens of *E*. *cellulosa*, and with type specimens of *Scirpus dictyospermus*, a name indicated first by Britton (1889) and later by Svenson (1929) to be synonymous with *E*. *cellulosa*. A review of numerous specimens referable to *E*. *cellulosa* in preparation for this study revealed various states in perianth bristle texture. Plants from throughout the distribution of *E*. *cellulosa* have perianth bristles that are narrow, smooth, or infrequently minutely nodulose (the dark brown nodules seen only at high magnification). However, Caribbean [*Correll 50733* (F, MO, NY)] and Puertorican [*Britton et al. 6636* (NY)] specimens were observed to have perianth bristles that are retrorsely spinulose from the tip to just below the middle. In these specimens, the spinules are readily observed at low magnification (10×), and the bristles are strap shaped, very similar to typical *E*. *mutata*. Finally, plants somewhat intermediate between these two forms with a few salient spinules at the tips of the bristles occur in specimens from the Yucatan Peninsula [*Novelo 337* (GH), *Espejo 1314* (MO), and *Trejo* 198 (MEXU)] and Cuba [*Wright 3763* (P)]. Interestingly, *S*. *dictyospermus* is based on *Wright 3763* from Cuba.

MATERIALS AND METHODS

Specimen Selection

Specimens of *Eleocharis cellulosa* including types and type specimens of *Scirpus dictyospermus* from the following herbaria were examined for this study: BRIT, CIIDIR, F, GA, GH, K, LL, P, MEXU, MICH, MO, NY, PH, SBSC, SMU, SWT, TAES, TEX, US, USF, VSC, and WIS. Sixty-five mature specimens (including four type specimens) that were complete for all selected characters and that originated from the Bahamas, Cuba, Florida, Mexico (Yucatan Peninsula), Puerto Rico, and Texas were selected for study. Thirteen specimens from Cuba, the Bahamas and Puerto Rico had achenes with one or more retrorsely spinulose perianth bristles.

Multivariate Analysis

Examination of herbarium specimens, including type specimens, resulted in the selection of 19 morphological characters for evaluation (Table 7). For each specimen, a spikelet with fully developed achenes was selected. For measurement of floral characters, an achene and its subtending scale were selected from near the base of the spikelet. Each specimen measured was complete for all characters so that the data matrix contained no missing values. A data matrix of multivariate observations for the 65 OTUs was explored using PCA. The principal components were generated using a correlation matrix. Scatter plots of the first three principal components were generated in an effort to evaluate the taxonomy of *Eleocharis celulosa*.

Table 7. Initial 19 characters used to evaluate morphological variation of *Eleocharis cellulosa*. All characters are continuous quantitative (CQ) except for BRSTACH, BRSTN, and LONROW which are discrete (D).

Symbol	**Character**	**Type**	**Unit**
ACHNBL	achene body length (from base to region of constriction at beak)	CQ	mm
ACHNBLW	ratio of achene body length to width (achene shape)	CQ	ratio
ACHNMAX	ratio of achene body length to distance from achene base to widest point (determines if achene is widest above, at, or below middle)	CQ	ratio
ACHNSCAL	ratio of achene length to floral scale length	CQ	ratio
ACHNW	achene body width (at widest point)	CQ	mm
BEAKL	beak length	CQ	mm
BEAKLW	ratio of beak length to beak width (beak shape)	CQ	ratio
BEAKW	beak width	CQ	mm
BEAKWACHW	ratio of beak width to achene width	CQ	ratio
BRSTACH	number of perianth bristles longer than summit of achene	D	number
BRSTLACHNBL	ratio of length of longest perianth bristle to achene body length	CQ	ratio
BRSTLNACHNL	ratio of number of perianth bristles longer than achene to total number of perianth bristles	CQ	ratio
BRSTN	number of perianth bristles	D	number
LONBRSTL	length of longest perianth bristle	CQ	mm
LONGROWS	longitudinal rows of cells on achene face	D	number
SCALEL	floral scale length	CQ	mm
SCALELW	ratio of floral scale length to width (floral scale shape)	CQ	ratio
SCALEW	floral scale width	CQ	mm
TBRCL	tubercle length	CQ	mm

RESULTS

Principal Components Analysis

The first three principal components explain 76.3% of the total variance (32.9%, 26.7%, and 16.7% for PC1, PC2, and PC3 respectively; Table 8). PCA axis 1 has high positive loadings for achene body length and achene width; PCA axis 2 has high positive loadings for beak length and beak shape (Table 8; Fig. 21). A scatter plot of the first two principal components (Fig. 22) with the OTUs labeled with geographical locations show no discernable infraspecific variation based on geographic distribution. All geographic populations overlap for the characters evaluated, and there is no indication of any geographical group forming a distinct cluster. Some variability occurs along PC axis 1 for Caribbean specimens and will be discussed below. The types of *Scirpus dictyospermus* also occur within the same area of points as the types of *Eleocharis cellulosa* indicating that the two names are equivalent for the morphological characters evaluated.

When the first two principal components are plotted in two-dimensions, and the first three principal components are plotted in three-dimensions and OTUs are labeled as either bristles smooth or one or more spinulose bristles present, the majority of the Caribbean specimens with retrorsely spinulose perianth bristles occur within the area of points occupied by OTUs with smooth perianth bristles (Fig. 23; Fig. 24). Five OTUs based on Caribbean specimens (*Correll 50733*; *Brace 2066*) with retrorsely spinulose perianth bristles occur

Table 8. Results of PCA of *Eleocharis cellulosa* for 9 variables of 65 OTUs.

	PC1	**PC2**	**PC3**
Eigenvalues	2.96	2.40	1.50
Component loadings			
ACHNBL	0.82	0.14	0.14
BEAKL	-0.17	0.93	-0.20
LONBRS	0.60	-0.19	-0.69
ACHNW	0.79	0.27	0.22
BEAKW	0.65	0.40	0.26
SCALEW	0.05	0.61	-0.40
ACHNSCAL	0.71	0.18	0.27
BRSTLNACHNL	0.47	-0.40	-0.74
BEAKLW	-0.35	0.83	-0.28
Percent of total variance explained	32.9	26.7	16.7

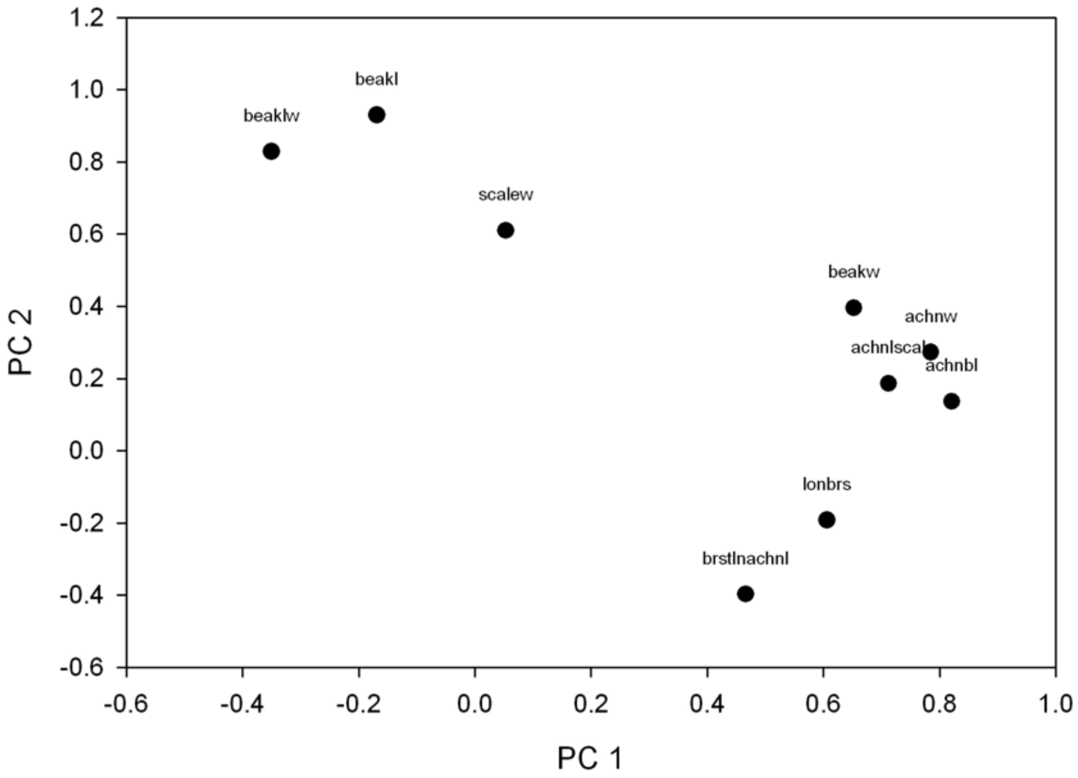


Fig. 21. PCA character loadings for analysis of *Eleocharis cellulosa*. Character abbreviations follow those from Table 7.

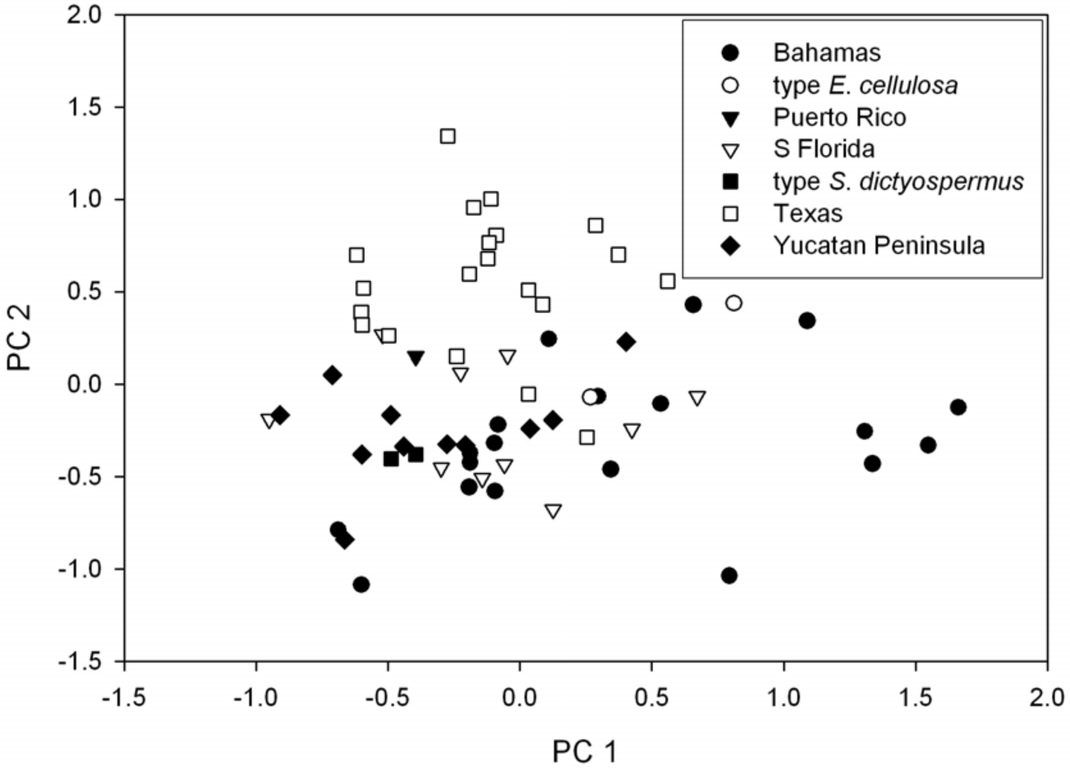


Fig. 22. Two-dimensional scatter plot of PCA ordination (PC1 vs. PC2) of geographic populations of *Eleocharis cellulosa*.

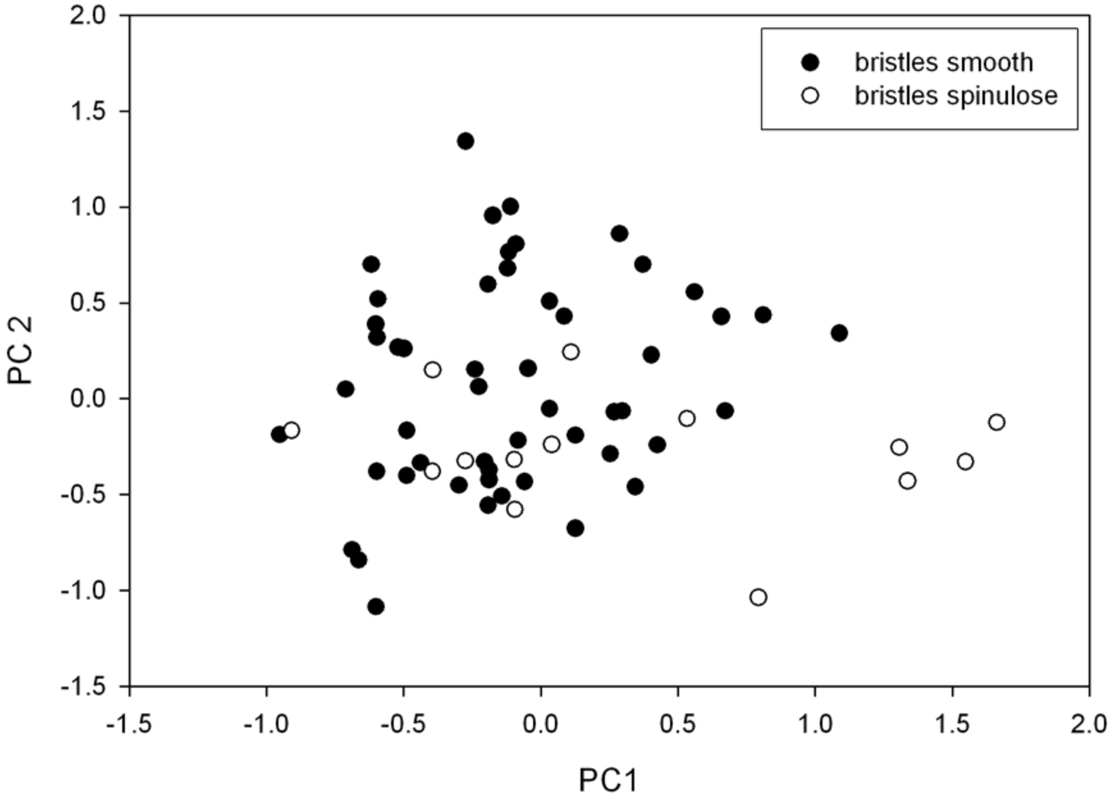


Fig. 23. Two-dimensional scatter plot of PCA ordination (PC1 vs. PC2) of bristle variants in *Eleocharis cellulosa*.

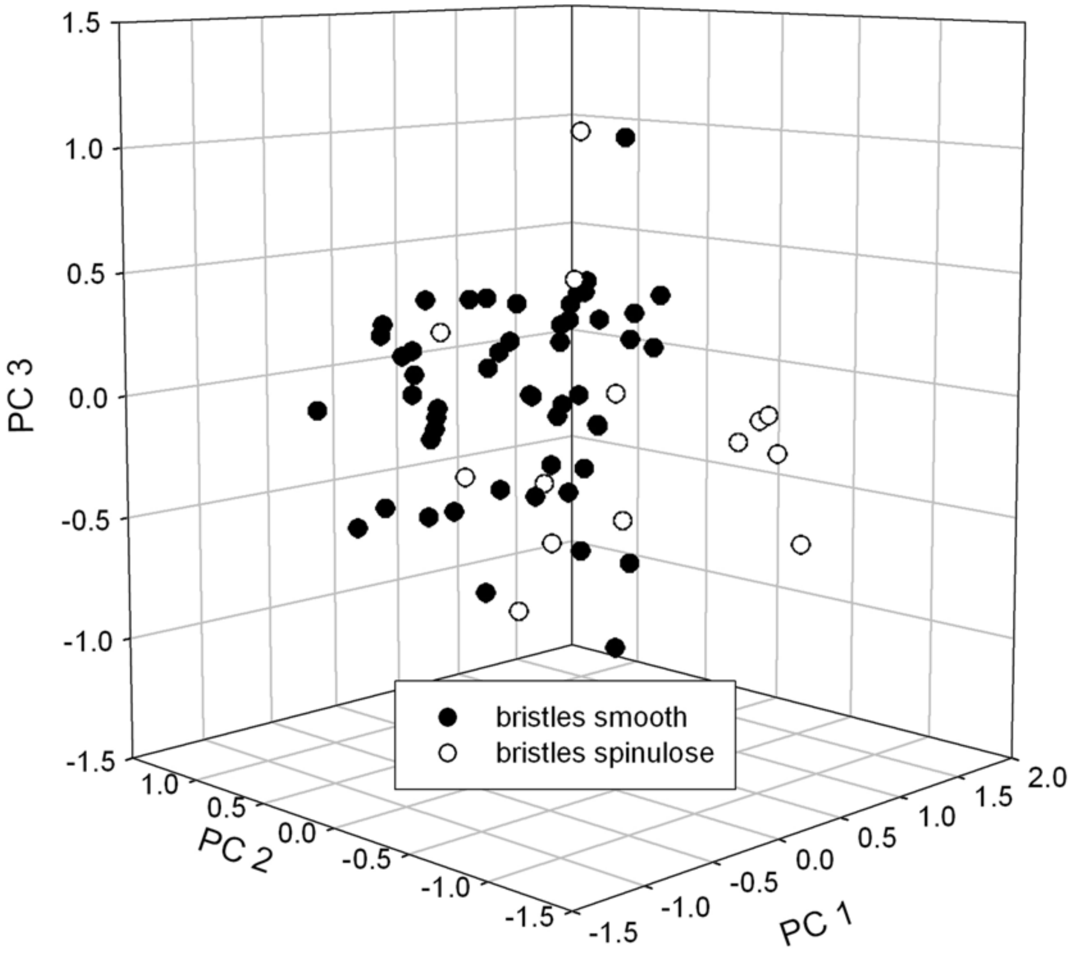


Fig. 24. Three-dimensional scatter plot of PCA ordination of perianth bristle forms of *Eleocharis cellulosa*.

outside the continuous area of points due to variability of achene body length and longest perianth bristle length (Fig. 23). The remaining characters account for the variability occurring within the relatively well delimited grouping of the other OTUs.

DISCUSSION AND CONCLUSIONS

Clear morphological separation among geographic populations of *Eleocharis celluolsa* could not be found. The PCA indicates that variation of the characters evaluated is well represented throughout the distribution of *E. cellulosa* and is scattered around the type specimens (Fig. 22). Occurrence of retrorsely spinulose bristles in a species known to typically have smooth bristles with an apparent geographic restriction to the islands of the Caribbean is noteworthy, but apparently does not warrant formal taxonomic recognition at this time based on the specimens studied.

This course is taken for several reasons as follows. Specimens of *Eleocharis cellulosa* examined with retrorsely spinulose bristles are syntopic with specimens with smooth bristles (Fig. 25), and differ by this one conspicuous character. The only appropriate rank for variation for a single, sympatric character (in this case the presence of spinules) would be forma. However Stuessy (1990) discourages the formal use of forma except in groups with important economic value.

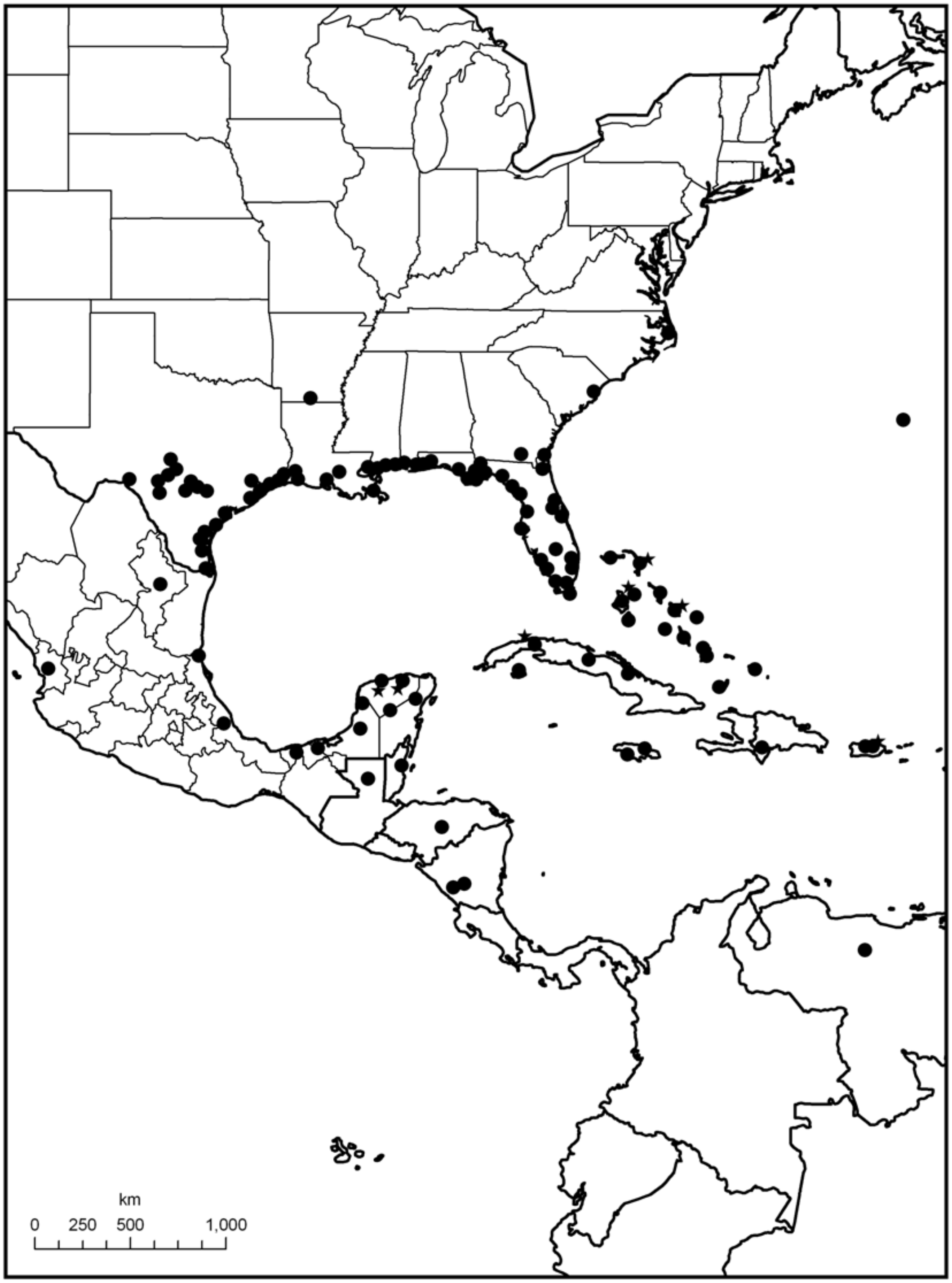


Fig. 25. Geographic distribution of *Eleocharis cellulosa* smooth bristle (●) and retrorsely spinulose bristle varients (⋆). Each dot represents the general geographic location of one or more specimens.

Indeed, the use of this rank in Cyperaceae has been scarcely used in the last few decades, and only two examples could be found in *Eleocharis*: *E*. *olivacea* Torr. forma *reductiseta* Schuyler & Ferrren (Schuyler and Ferren 1975) and *E*. *geniculata* (L.) Roem. & Schult. forma *brunnea* S. González & Reznicek (González-Elizondo and Reznicek 1996). Schuyler and Ferren (1975) based their new taxon solely on difference in perianth bristle length and texture.

Careful review of specimens during this study revealed that achenes possessing either smooth or retrorsely spinulose bristles could occur on different accessions of the same collection, and on different achenes from the same spikelet. Indeed, in most cases a mixture of smooth and spinulose bristles can occur on the same achene. The occurrence of a series of the same collectors number deposited in different herbaria in which one sheet has achenes possessing smooth bristles, and another with achenes possessing retrorsely spinulose bristles could result in annotating two different accessions of the same collection collected at the same time and place as different taxa; an undesirable and counterproductive outcome.

This study suggests that *Eleocharis cellulosa* is represented by a single taxon distributed in coastal areas of the southeast United States, The Caribbean, Mexico, Central America, and northern South America with an apparent Caribbean genotype distinguished by variously retrorsely spinulose perianth bristles. The presence of smooth perianth bristles in *E*. *cellulosa* is probably phylogenetically significant since most other species in subgenus

Limnochloa have retrorsely spinulose perianth bristles. Additional studies would be useful if more Caribbean specimens with retrorsely spinulose perianth bristles could be obtained. Those specimens observed during this study with achenes possessing both smooth and retrorsely spinulose bristles could prove to be intermediate between two extreme and stable forms suitable for formal recognition.

CHAPTER VI

MORPHOMETRIC NUMERICAL STUDY OF WORLDWIDE VARIABILITY OF *ELEOCHARIS ACUTANGULA*

INTRODUCTION

Eleocharis acutangula sensu lato (s.l.) is pantropic in distribution. Based on Svenson (1939, map 28) and review of herbarium specimens, it appears to be the most widely distributed species of *Eleocharis* subg. *Limnochloa*. Label data from the specimens studied also suggest that it might have the widest ecological amplitude of the species treated during this research. In the New World it is reported from near sea level to 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. *Eleocharis acutangula* has also the most extensive synonymy of any of the species studied herein, which apparently results partly from a wide distribution and partly from morphological variation.

Eleocharis acutangula is usually regarded as an Old World species, and indeed it and all of its current synonyms are based on Old World collections from Africa, India, Madagascar, and Java. Barros (1960) treated *E*. *obtusetrigona* of the New World as a variety of *E*. *fistulosa*. However, previous studies (González-Elizondo et al. 2002; Rosen and Hatch 2006) along with achene macro- and micromorphological characters (see Chapter II) and field observations in Mexico support its recognition as a distinct species. Several authors have reported considerable variation in *E*. *acutangula* (Svenson 1929, 1939; Haines & Lye 1983; Browning et al. 1997). In his monograph of *Eleocharis*, Svenson (1929, 1939) indicated several potential segregates of *E*. *fistulosa* (e.g. *E*. *planiculmis*, *E*. *fistulosa* var. *robusta*) and described a great deal of morphological variability in Old World and New World plants generally referable to *E*. *acutangula*. Hess (1953) described *Heleocharis pseudofistulosa* H. Hess. based on plants he collected in Angola, and stated they differed from *E. fistulosa* in the surface sculpturing of the achene. Hess (1957) later reported an entity he provisionally assigned as *H*. cf *pseudofistulosa* from South America (Brazil), which he described to differ from *H*. *pseudofistulosa* in having terete rather than sharply three-angled culms (presumably *E*. *obtusetrigona*). Hess (1953) also raised *E*. *fistulosa* var. *robusta* to the rank of species under *Heleocharis*.

Svenson (1939) listed *E*. *fistulosa* as being among several tropical African species that were not well defined. Browning et al. (1997) described variability among specimens of *E*. *acutangula* from different geographic areas in Africa. This study, including review of over 600 herbarium specimens, confirms the situation described above. No study of the cosmopolitanism of *E*. *acutangula* has been published. Indeed, it is proposed herewith that the specimens currently referable to *E*. *acutangula* s.l. are actually a complex of three species, *E*. *acutangula*, *E*. *neotropica* sp. nov., and *E*. *steinbachii* sp. nov., and that *E*. *acutangula* comprises at least two infraspecific segregates. Additionally, the lack of a designated type specimen for *E*. *acutangula* potentially adds instability to the definition of the species and its relationship with currently accepted synonyms.

The objectives of this study were to use morphometric numerical analysis to better define *Eleocharis acutangula*, determine if a practical infraspecific taxonomic separation could be found (and if so, what rank is appropriate for the segregate taxa), and study its relationship with *E*. *fistulosa*, *E*. *planiculmis*, *E*. *fistulosa* var. *robusta*, *E*. *neotropica* sp. nov., *E*. *steinbachii* sp. nov., and *Heleocharis pseudofistulosa*. Distribution maps were also plotted in an effort to study range and distribution, elucidate nativity and origin, and predict patterns of introduction.

MATERIALS AND METHODS

Herbarium Selection

For this study, specimens were borrowed from large domestic and foreign herbaria that could provide loans yielding good geographical representation of *Eleocharis acutangula*. Additional selection criteria included herbaria where types or otherwise notable specimens were housed as they came to light following an extensive literature review and correspondences with cyperologists worldwide. Over 600 specimens were examined from the following herbaria: BM, BRI, BRIT, C, CIIDIR, CM, E, F, FTG, GA, GH, IBE, K, LL, M, MEXU, MICH, MO, NH, NU, NY, P, PH, PRE, RSA, TAES, TEX, US, USF, VSC, WIS, Z, and ZT.

Populations

Herbarium studies and field work in 2004 resulted in the discovery of plants referable to *Eleocharis acutangula* in Lee County, Florida, and collections were made of a population comprising 10 reproductively mature specimens. Additional artificial populations were established from the herbarium specimens available for study. Selected for analysis were 205 mature specimens referable to *E*. *acutangula* s.l. (including types) complete for all characters measured. Material studied originated from a wide geographical area and comprised specimens from Africa, Australia, Bolivia, Brazil, China, Colombia, Cuba, Dominican Republic, Ecuador, El Salvador, Guyana, India, Japan, Madagascar, Malesia, Panama, Peru, United States, Venezuela, and Vietnam. Specimens were assigned *a-priori* to either *E*. *acutangula* subsp. *acutangula*, *E*. *acutangula* subsp. *breviseta* subsp. nov., *E*. *neotropica* sp. nov., or *E*. *steinbachii* sp. nov. before the morphological characters were measured. This was done to determine if groups revealed by PCA agreed with the *a-priori* assignment.

Multivariate Analysis

Examination of live plants of *Eleocharis acutangula* in the field and greenhouse-grown specimens, along with study of herbarium specimens (including types) resulted in selecting 20 morphological characters for initial evaluation (Table 9). For each specimen, a spikelet with fully developed achenes was selected. For measurement of floral characters, an achene and its subtending scale were selected from near the base of the spikelet. Each specimen measured was complete for all characters so that the data matrix contained no missing values.

Table 9. Initial 20 characters used to evaluate morphological variation of the *Eleocharis acutangula* complex and infraspecific variation within *E*. *acutangula*. All characters are continuous quantitative (CQ) except for BRSTACH, BRSTN, and LONROW which are discrete (D).

Symbol	**Character**	**Type**	**Unit**
ACHNBL	achene body length (from base to constriction at neck)	CQ	Mm
ACHNBLW	ratio of achene body length to width (achene shape)	CQ	Ratio
ACHNMAX	ratio of achene body length to distance from achene base to widest point (determines if achene is widest above, at, or below middle)	CQ	Ratio
ACHNSCAL	ratio of achene body length to floral scale length	CQ	Ratio
ACHNW	achene body width (at widest point)	CQ	Mm
BRSTACH	number of perianth bristles longer than summit of achene	D	number
BRSTLACHNBL	ratio of length of longest perianth bristle to achene body length	CQ	Ratio
BRSTLNACHNL	ratio of number of perianth bristles longer than summit of achene to total number of perianth bristles	CQ	Ratio
BRSTN	number of perianth bristles	D	number
LONBRSTL	length of longest perianth bristle	CQ	Mm
LONROW	number of longitudinal rows of cells on achene face	D	number
NECKACHNW	ratio of neck width to achene width	CQ	Ratio
NECKW	neck width	CQ	Mm
SCALEL	floral scale length	CQ	Mm
SCALELW	ratio of floral scale length to width	CQ	Ratio
SCALEW	floral scale width	CQ	Mm
TBRACHW	ratio of tubercle width to achene width	CQ	Ratio
TBRCL	tubercle length	CQ	Mm
TBRCLW	ratio of tubercle length to width	CQ	Ratio
TBRCW	tubercle width	CQ	Mm

For the first analysis, a total of 205 OTUs were numerically analyzed in order to distinguish *Eleocharis neotropica* sp. nov., or *E*. *steinbachii* sp. nov. from *E*. acutangula. A second analysis comprising 178 OTUs was run to determine if a satisfactory infraspecific taxonomic separation could be achieved.

The raw morphometric data were standardized and analyzed by PCA using NTSYSpc 2.11Q (Rohlf 2000). The principal components were generated using a correlation matrix. For both analyses, the initial character set was scored using PCA, and characters found to be highly intercorrelated or with low loadings were removed and the analysis re-run. For each analysis, a scree plot was generated to determine how many principal components to extract (Rencher 1998). Two and three-dimensional scatter plots of the principal components were generated in an effort to depict taxonomic novelties and infraspecific taxa in the *Eleocharis acutangula* complex.

RESULTS

Eleocharis acutangula Complex

The first three principal components explain 81.8% of the total variance (39.8%, 26.9%, and 15.1% for PC1, PC2, and PC3 respectively; Table 10) of 205 OTUs scored for 11 morphological characters. Principal components 1 & 2 account for 66.7% of the total variability within the data. However, principal components 2 & 3 are the most useful for examining morphological characters that distinguish *Eleocharis neotropica* and *E*. *steinbachii* from *E*. *acutangula*. PCA axis 2 is most influenced by high positive loadings of tubercle shape (tubercle length/tubercle width) and tubercle length, and high negative loadings of the ratio of tubercle width to both achene width and neck width. PCA axis 3 is most highly influenced by high positive loadings of achene width and high negative loadings of the ratio of the length of the longest perianth bristle to the achene body length (Fig. 26; Table 10). Two- and three-dimensional scatter plots of the second and third principal components (Fig. 27, Fig. 28) show a distinct cluster of points representing *E*. *neotropica* and a cluster of points for *E*. *steinbachii* that overlap with *E*. *acutangula*.

Table 10. Results of PCA of *Eleocharis acutangula* complex for 11 variables of 205 OTUs.

	PC1	**PC2**	**PC3**
Eigenvalues	4.38	2.96	1.66
Component Loadings			
ACHNBL	0.63	0.26	0.52
ACHNW	0.69	0.04	0.59
BRSTACH	0.72	0.37	-0.47
BRSTLACHBNL	0.74	0.28	-0.58
LONBRSTL	0.82	0.34	-0.40
NECKWACHNW	0.51	-0.66	-0.24
NECKW	0.77	-0.51	0.11
TBRCWACHNW	0.35	-0.76	-0.07
TBRCL	0.54	0.53	0.36
TBRCLW	0.20	0.81	0.18
TBRCW	0.69	-0.59	0.29
Percent of total variance explained	39.8	26.9	15.1

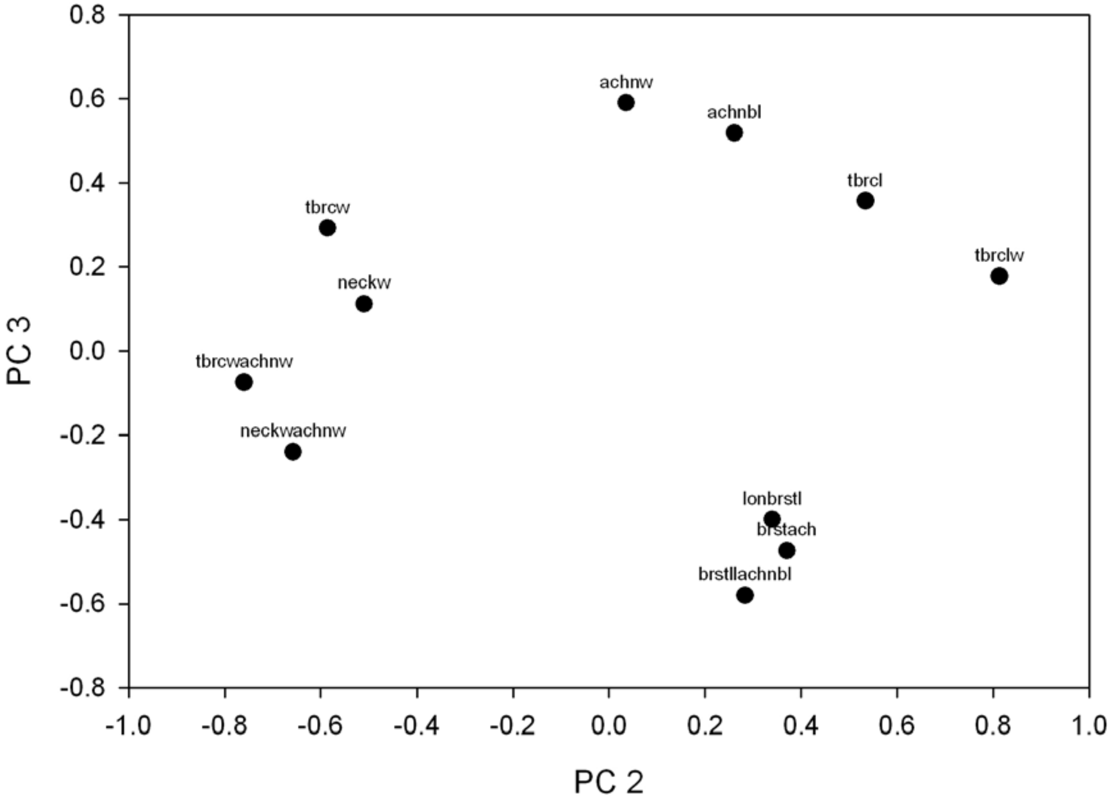
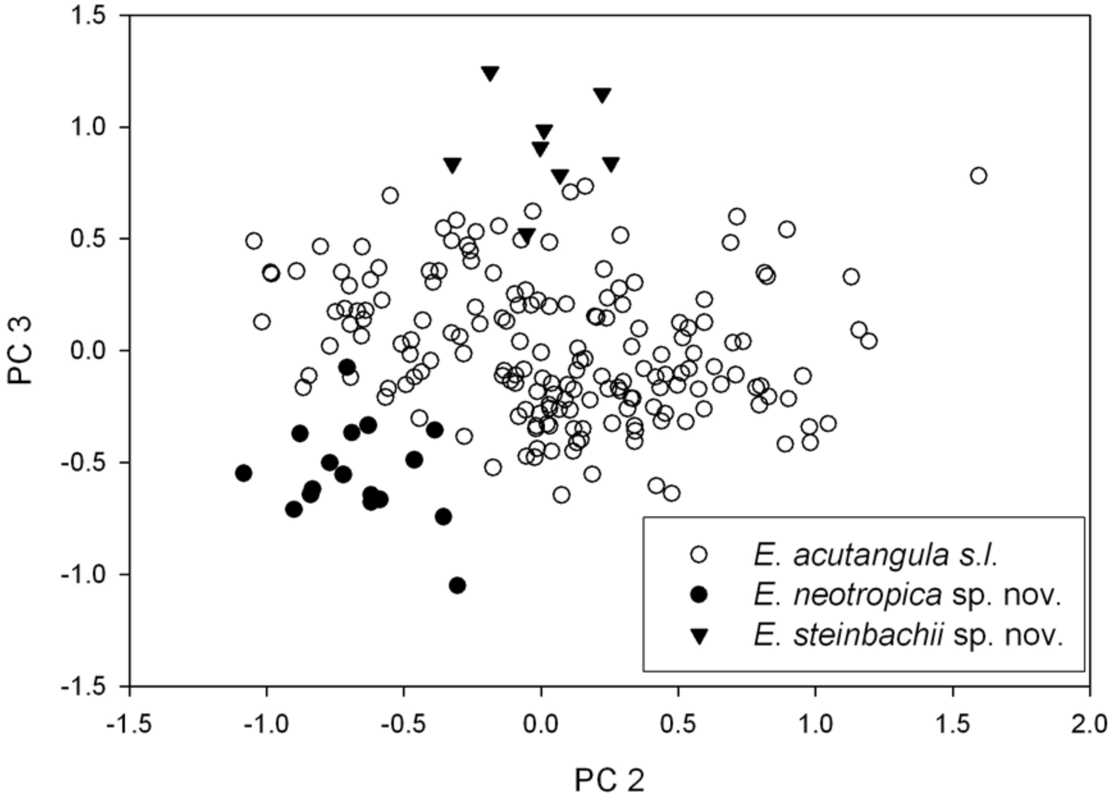


Fig. 26. PCA character loadings (PC2 vs. PC3) for analysis of *Eleocharis acutangula* complex. Character abbreviations follow those from Table 9.



-

Fig. 27. Two-dimensional scatter plot of PCA ordination (PC2 vs. PC3) depicting separation of *Eleocharis neotropica* and *E*. *steinbachii* from *E*. *acutangula*.

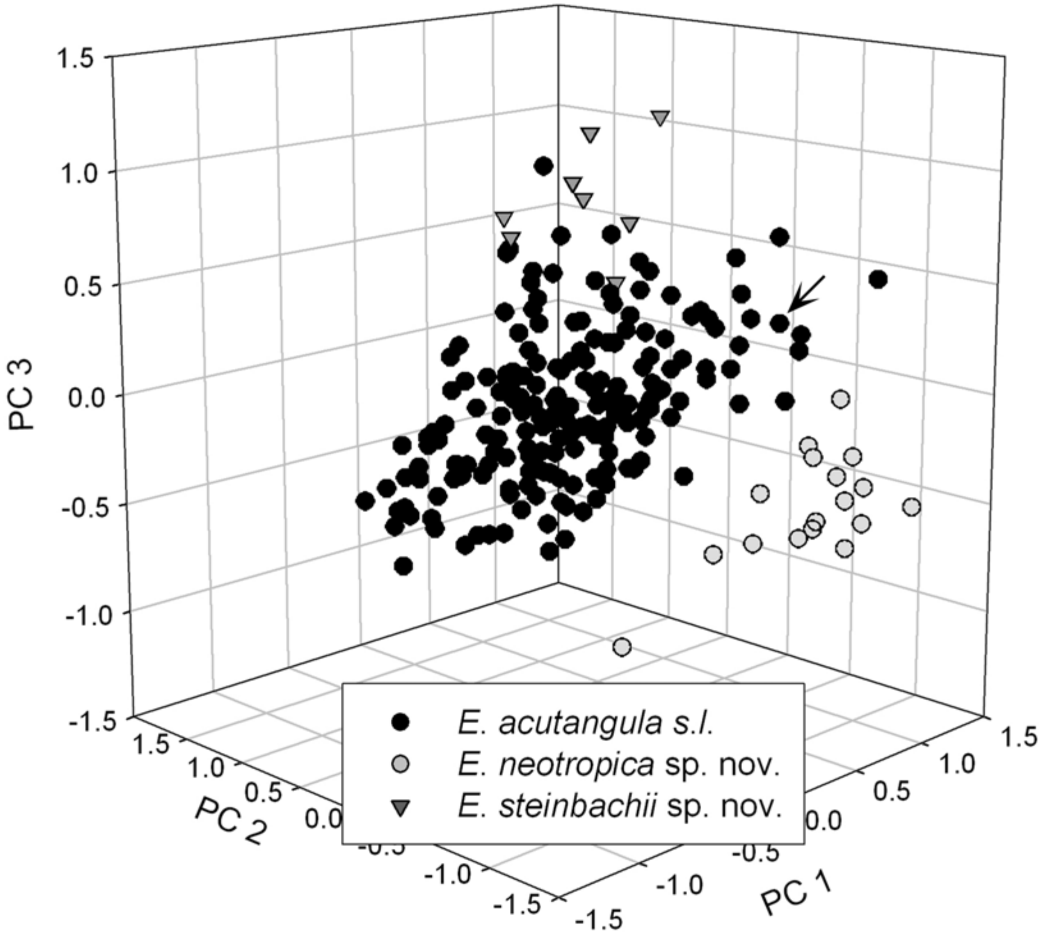


Fig. 28. Three-dimensional scatter plot of PCA ordination depicting separation of *Eleocharis neotropica* and *E*. *steinbachii* from *E*. *acutangula*. Arrow indicates proposed lectotype of *E*. *acutangula* subsp. *acutangula*.

Infraspecific Variation in *Eleocharis acutangula*

The first three principal components explain 89.5% of the total variance (59.4%, 19.8%, and 10.3% for PC1, PC2, and PC3 respectively; Table 11) of 178 OTUs scored for 8 morphological characters. Principal components 1 & 2 account for 79.2% of the total variability within the data. PCA axis 1 is most influenced by high positive loadings of longest perianth bristle length, the ratio of longest perianth bristle length to achene body length, the number of perianth bristles exceeding the summit of the achene, tubercle length, achene body length, and tubercle shape (tubercle length/tubercle width) (Fig. 29; Table 11). The variation observed along PCA axis 2 indicates those characters most variable within each infraspecific segregate, and includes high positive loadings for achene width, achene body length, and floral scale length (Fig. 30; Table 11). Two-dimensional scatter-plots of principal components 1 vs. 2 and 1 vs. 3 are both useful for examining separation and morphological characters that distinguish *Eleocharis acutangula* subsp. *acutangula* and *E*. *acutangula* subsp. *breviseta* since most of the variability between these two segregates is explained by PCA axis 1 (Figs. 30 and 31). A three-dimensional scatter plot shows the relatively small area occupied by *E*. *acutangula* subsp. *breviseta* compared to that occupied by *E*. *acutangula* subsp. *acutangula* and types of its synonyms (Fig. 32).

Table 11. Results of PCA of *Eleocharis acutangula* subsp. *acutangula* and *E. acutangula* subsp. *breviseta*. for 8 variables of 178 OTUs.

	PC1	**PC2**	**PC3**
Eigenvalues	4.75	1.58	0.83
Component Loadings			
ACHNBL	0.73	0.56	-0.11
ACHNW	0.60	0.68	0.01
BRSTACH	0.83	-0.28	-0.39
BRSTLACHBNL	0.87	-0.36	-0.27
LONBRSTL	0.94	-0.16	-0.25
SCALEL	0.61	0.58	0.23
TBRCL	0.82	-0.20	0.46
TBRCLW	0.70	-0.46	0.51
Percent of total variance explained	59.4	19.8	10.3

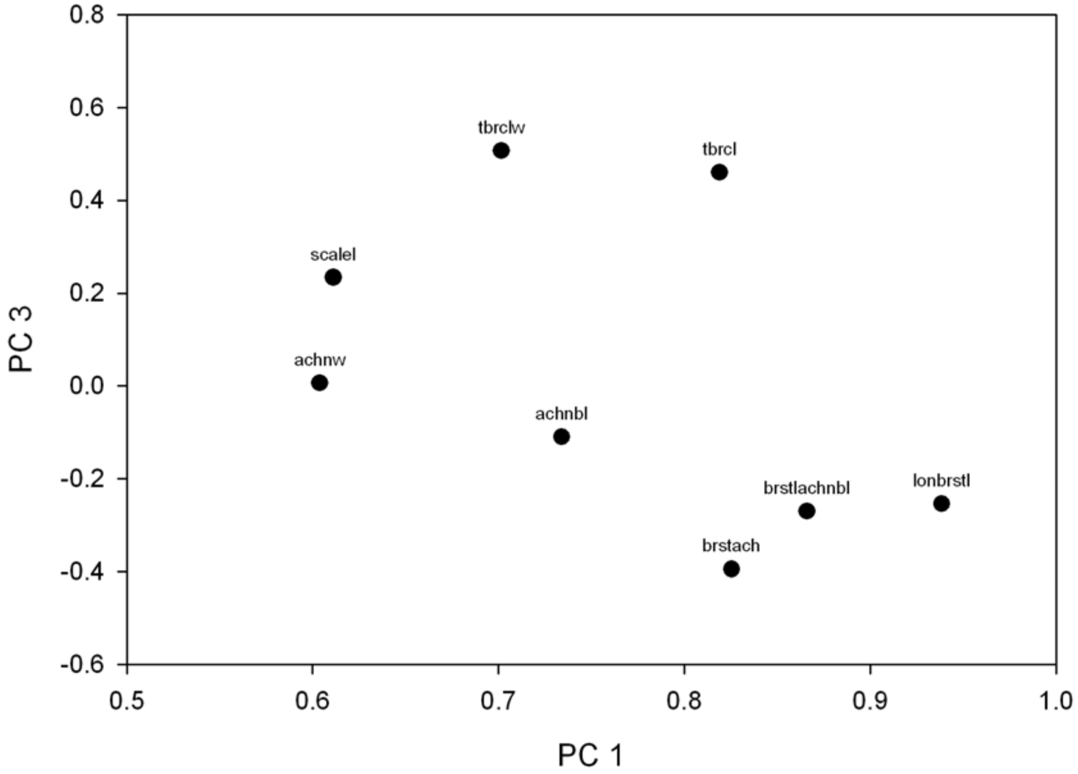


Fig. 29. PCA character loadings (PC1 vs. PC3) for analysis of *Eleocharis acutangula* subsp. *acutangula* and *E*. *acutangula* subsp. *breviseta*. Character abbreviations follow those from Table 9.

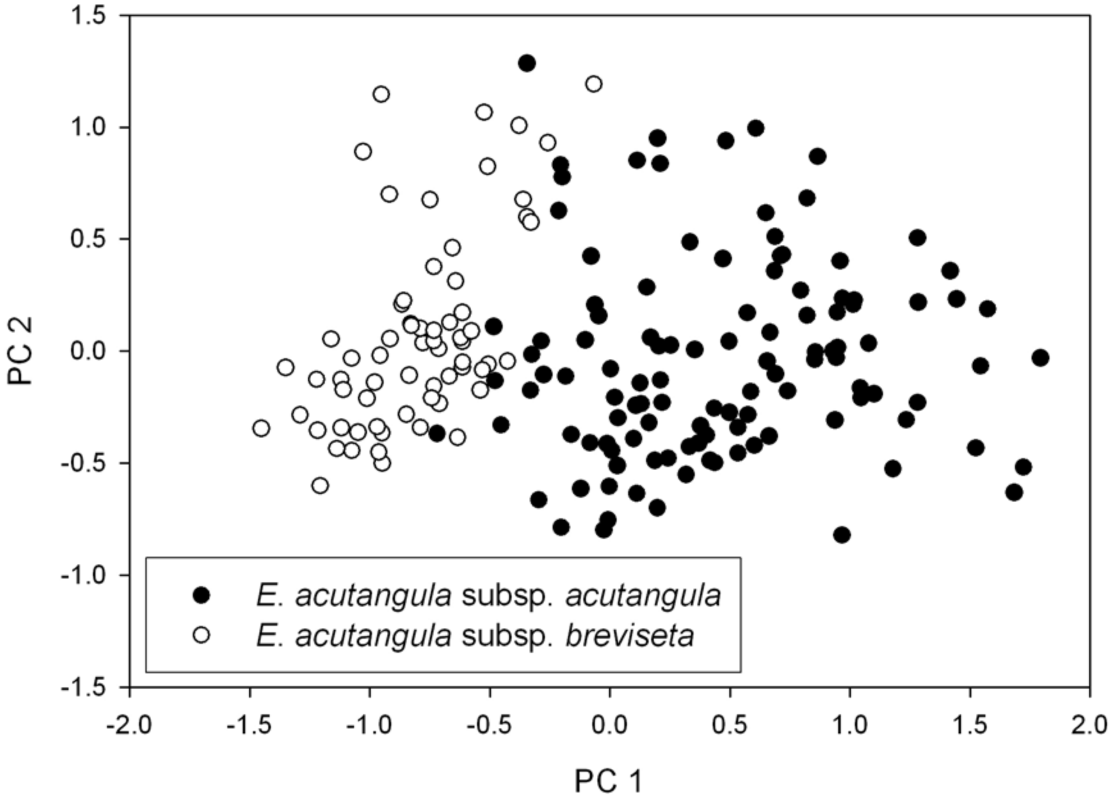


Fig. 30. Two-dimensional scatter plot of PCA ordination (PC1 vs. PC2) depicting separation of *Eleocharis acutangula* subsp. *acutangula* and *E*. *acutangula* subsp. *breviseta*.

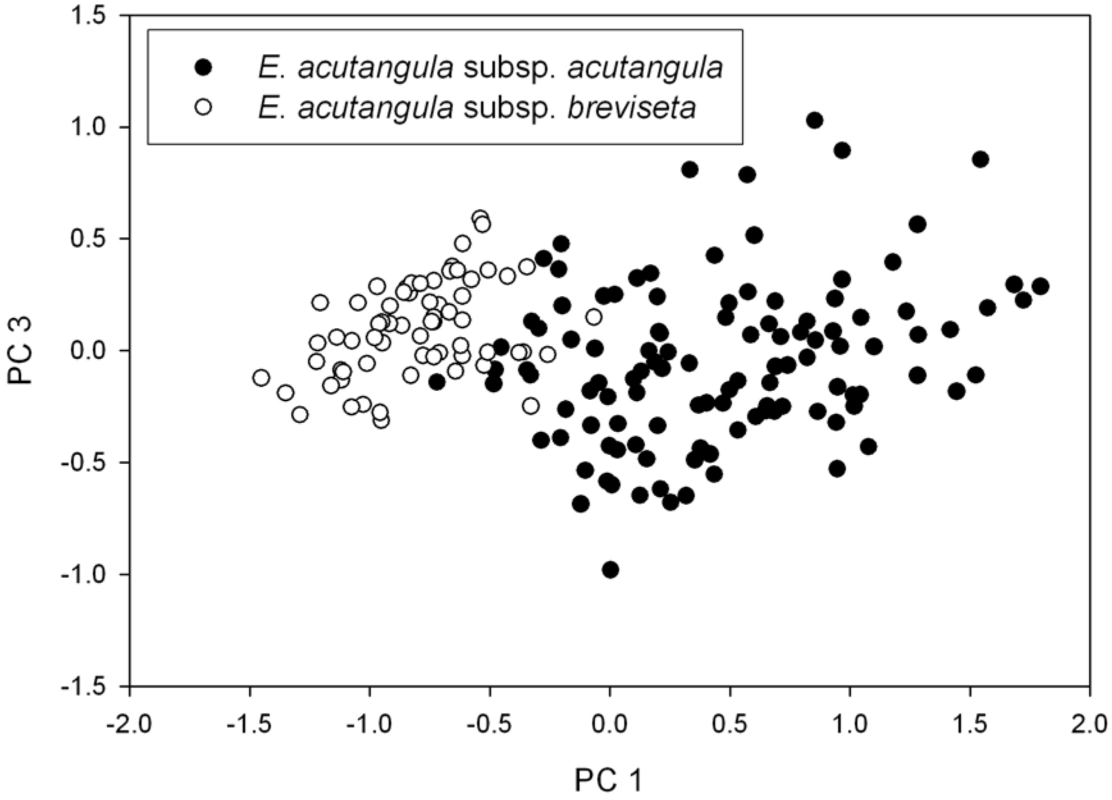


Fig. 31. Two-dimensional scatter plot of PCA ordination (PC1 vs. PC3) depicting separation of *Eleocharis acutangula* subsp. *acutangula* and *E. acutangula* subsp. *breviseta*.

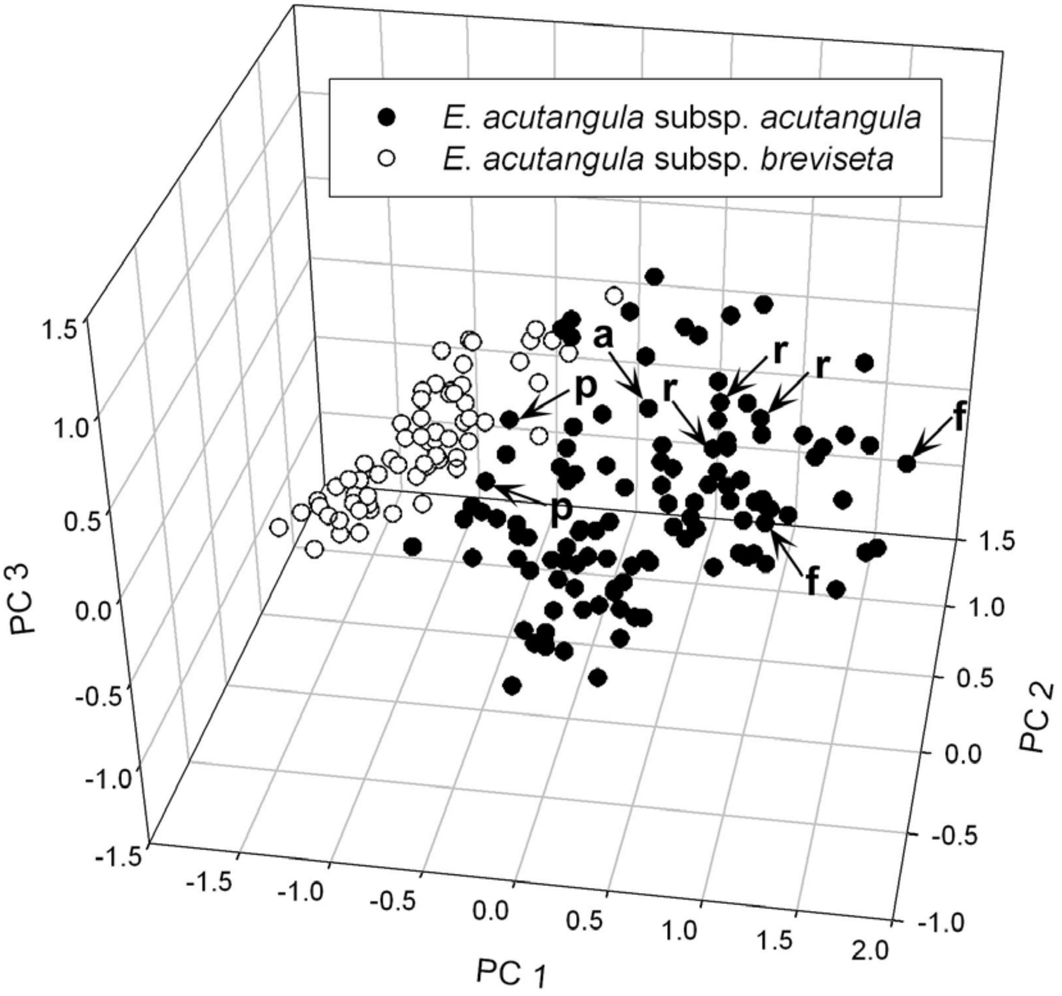


Fig. 32. Three-dimensional scatter plot of PCA ordination depicting separation of *Eleocharis acutangula* subsp. *acutangula* and *E*. *acutangula* subsp. *breviseta*. Arrows indicate (**a**) proposed lectotype of *E*. *acutangula* subsp. *acutangula*; (**f**) types of *E*. *fistulosa*; (**p**) types of *E*. *planiculmis*; and (**r**) types of *E*. *fistulosa* var. *robusta*.

DISCUSSION AND CONCLUSIONS

A summary of the characters accounting for most of the variability in the multivariate analysis, along with a qualitative description of the texture of perianth bristle spinules, suggests that features of the mature achene and perianth are essential for identification of the segregates identified within *Eleocharis acutangula* s.l. (Table 12). Characters such as achene shape or dimensions of the floral scales did not prove useful for distinguishing among these closely related taxa. The recognition of *E*. *neotropica* as a distinct species is supported as it forms a distinct cluster when viewed in the three-dimensional scatter plot (Fig. 28), and is readily distinguished from *E*. *acutangula* and *E*. *steinbachii* by its very long and coarsely retrorsely spinulose perianth bristles (on average 2 times or longer than the achene body), the neck half or more wide than the width of the achene, the tubercle wider than tall with a truncate or retuse apex, and a distribution restricted to northwestern South America (Fig. 33). The achenes of *E*. *steinbachii* are slightly longer and wider, and the tubercle is longer than in the other species of this complex (Table 12). Although *E*. *steinbachii* overlaps to some degree with *E*. *acutangula* when viewed in a two- or three-dimensional scatter plots (Figs. 27 and 28), its recognition as a distinct species is supported by several morphological features and its narrow distribution.

Table 12. Selected character comparisons for *Eleocharis acutangula* and segregates. Means and ranges (mean ± 1 standard deviation) are provided for quantitative characters.

Character	***E. acutangula* subsp. *acutangula***	***E. acutangula* subsp. breviseta**	***E. steinbachii***	***E. neotropica***
achene body length (mm)	1.8 1.6-2	1.6 1.4-1.7	2.0 1.8-2.1	1.7 1.6-1.8
achene body width (mm)	1.4 1.3-1.6	1.3 1.2-1.4	1.5 1.4-1.6	1.4 1.3-1.5
ratio of length of longest perianth bristle to achene body length	1.5 1.1-1.8	0.8 0.6-0.9	0.6 0.4-0.7	2 1.9-2.3
length of longest perianth bristle (mm)	2.6 2-3.2	1.2 1.0-1.5	1.1 0.7-1.4	3.6 3.2-4
number of longitudinal rows of cells on achene face	14 13-15	13 11-14	20 18-22	13 12-14
ratio of neck width to achene width	0.4 0.3-0.4	0.4 0.3-0.4	0.4 0.3-0.4	0.5 0.5-0.6
description of perianth bristle spinules	coarsely retrorse nearly to the base or less often completely smooth	only a few short, salient retrorse spinules near the tips	mostly spreading (a few may be retrorse or antrorse)	coarsely retrorse nearly to the base
ratio of tubercle width to achene width	0.5 0.5-0.6	0.5 0.5-0.6	0.6 0.5-0.6	0.6 0.6-0.7
tubercle length (mm)	0.6 0.5-0.8	0.4 0.3-0.5	0.8 0.7-0.9	0.5 0.4-0.5
ratio of tubercle length to width (tubercle shape)	0.9 0.6-1.1	0.6 0.5-0.8	0.6 0.5-0.6	0.5 0.4-0.6

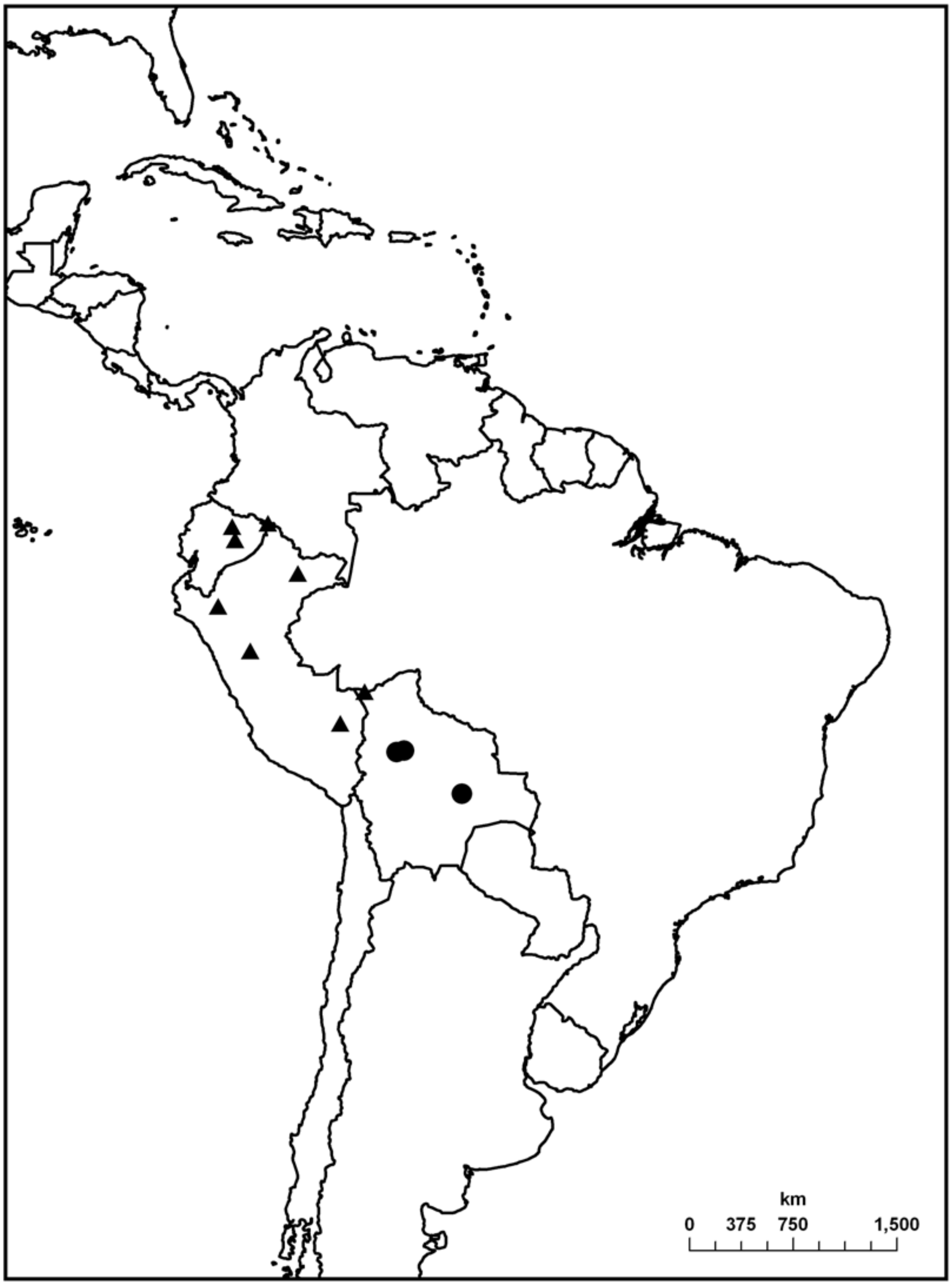


Fig. 33. Geographic distribution of *Eleocharis neotropica* (▲) and *E*. *steinbachii* (●). Each dot represents the general geographic location of one or more specimens.

Achenes of *E*. *steinbachii* have short, stiff perianth bristles with mostly spreading spinules and more numerous (18-22) longitudinal rows of small, transversely oblong polygonal cells on the achene face giving it a smooth, finely striated appearance.

The known distribution of *E*. *steinbachii* is restricted to the Llanos de Mojos region of northern Bolivia (Fig. 33). Indeed, the restricted geographical distributions of *E*. *neotropica* and *E*. *steinbachii* may provide prezygotic isolation between these two species and from *E*. *acutangula*, although this theory needs study since little nothing is known about the habitat of the species beyond sparse label data. All specimens of *E*. *steinbachii* studied had a conspicuously forked perianth bristle adaxially. However, more specimens of *E*. *steinbachii* need to be studied to determine the reliability of this character since it has also been very rarely observed in *E*. *acutangula*.

Within *Eleocharis acutangula*, two infraspecific taxa are distinguishable by multivariate analysis. The presence of several conspicuous morphological differences between these two forms, a relatively cohesive distribution of each and peripatric distribution of both (Fig. 34) suggests subspecies is an appropriate rank for classification (Stuessy 1990). *Eleocharis acutangula* subsp. *breviseta* is best distinguished from the nominal subspecies by its short perianth bristles with only a few short, salient retrorse spinules near the tips.

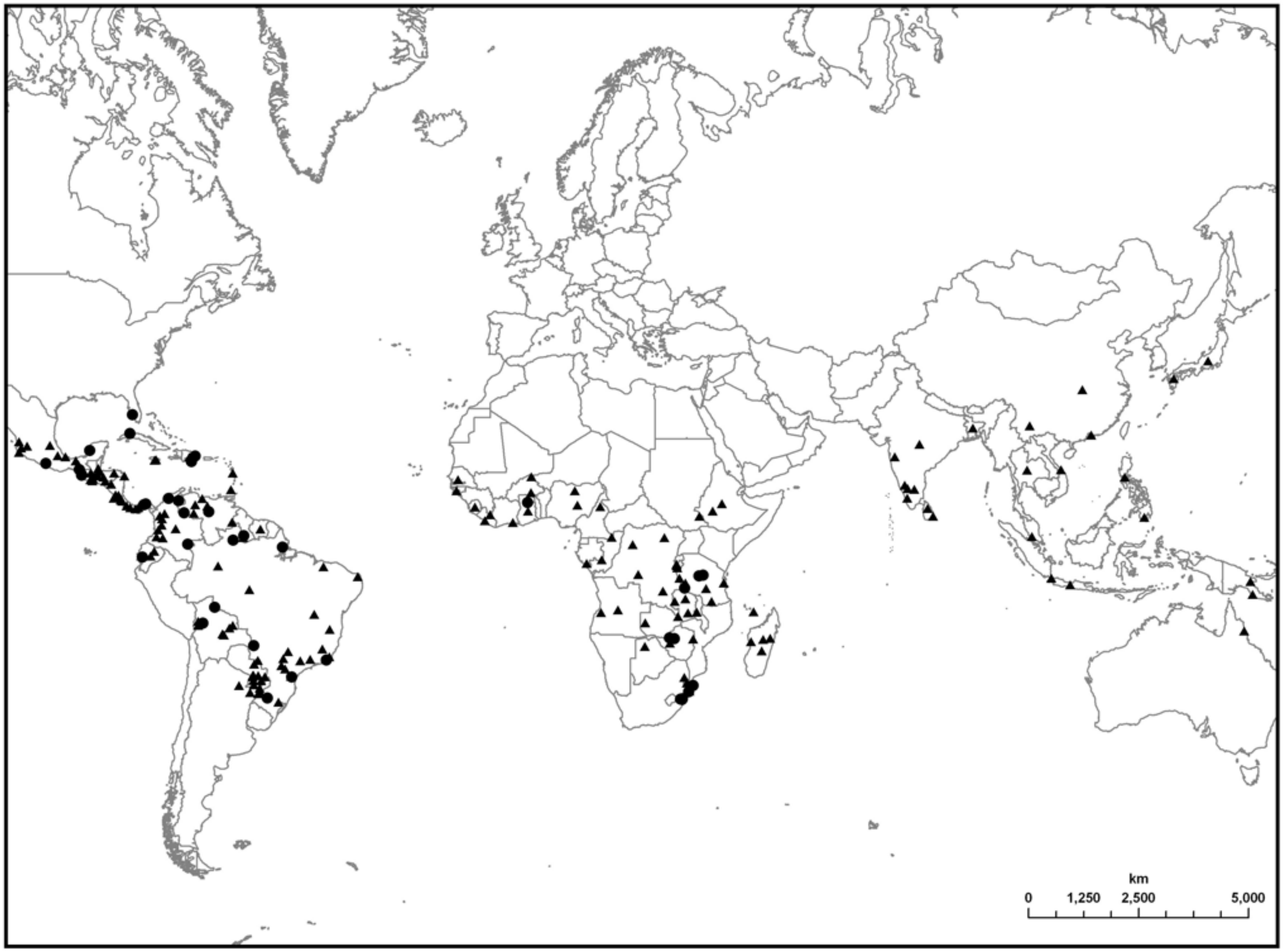


Fig. 34. Geographic distribution of *Eleocharis acutangula* subsp. *acutangula* (▲) and *E. acutangula* subsp. *breviseta* (●). Each dot represents the general geographic location of one or more specimens.

A number of the parameters evaluated by multivariate analysis are overlapping between subsp. *breviseta* and subsp. *acutangula* (Table 12). However, the achene bodies of subsp. *breviseta* are on average shorter and narrower, and the tubercles are on average shorter and have a smaller length-to-width ratio (Table 12).

One specimen, *Adams 4201* (NY) from Ghana, was dubiously assigned *a-priori* to *E*. *acutangula* subsp. *breviseta* because of its rudimentary to very short perianth bristles and disjunct distribution. However, this specimen occurs within the cluster of points referable to subsp. *breviseta*. The limited distribution of *E*. *acutangula* subsp. *breviseta* in southern Africa suggests that it was probably introduced there by long-range dispersal.

More variability was observed in specimens referable to *Eleocharis acutangula* subsp. *acutangula* for several of the parameters used in the multivariate analysis including achene dimensions, perianth bristle length, tubercle length and shape (Fig. 30; Fig. 31; Table 12). During examination of specimens for *a-priori* assignment, variability was also observed in achene surface sculpturing and epidermal cell shape, often in achenes from the same accession (refer to discussion in Chapter II). Svenson (1929; 1939) suggested that *E*. *fistulosa* var. *robusta* and *E*. *planiculmis* possibly represented distinct species from *E*. *acutangula*. However, the position of the type specimens in the three-dimensional scatter plot (Fig. 32) along with critical examination suggests that they are referable to *E*. *acutangula* subsp. *acutangula*. The achenes of *E*.

planiculmis appear to be immature; thus, their small size and poorly developed perianth bristles artificially place them in a position near subsp. *breviseta* (Fig. 32). The type specimens of *E*. *fistulosa* fall within the grouping of points representing *E*. *acutangula* subsp. *acutangula*. A small sample of specimens from Madagascar [*DuPuy 2429* (MO, K, P); *Bathie 17929* (P, US); and *Bathie 2722* (P)] including the type specimens of *E*. *fistulosa* possessed culms with the distal portion trigonous with the angles smooth and obtuse rather than triquetrous with the angles sharp and winged (as in all other specimens of *E*. *acutangula* examined). Indeed, the protologue of *E*. *fistulosus* describes the culms as “subtriquetro”. These specimens are otherwise referable to *E*. *acutangula* subsp. *acutangula* for the characters used in the multivariate analysis. For the time being this name is not proposed to be re-segregated on the basis of a single vegetative character and review of such a limited number of specimens. However, following further study it could be warranted.

This morphometric numerical analysis of *Eleocharis acutangula* s.l. supports it’s segregation into two infraspecific taxa and two new species, *E*. *neotropica* and *E*. *steinbachii*. This study also demonstrates the usefulness of PCA for analyzing and viewing a summary of multiple morphological characters simultaneously. Confident identifications of the members of this complex can only be made by carefully studying mature achenes. This is a common predicament found in other species complexes comprising closely related taxa in Cyperaceae.

Eleocharis acutangula has traditionally received attention as a paleotropical species, and indeed it is widespread in the Old World (Fig. 34). Prior to this study it was thought to be of Old World origin. The description of two new species with a narrow distribution in northwestern South America, and an infraspecific taxon with its distribution centered in the New World Tropics calls into question this assumption. Indeed, other species restricted to the New World share several morphological synapomorphies with *E*. *acutangula* (i.e., floral scales with coarse, distinctly raised veins, an achene apex markedly constricted into a distinct neck, tubercles distinct and greatly dorsoventrally compressed, and the presence of wing like remnants on the rachilla joints). *Eleocharis acutangula* and the new taxa defined herewith, combined with *E*. *elongata* Chapm., *E*. *liesneri*, *E*. *obtusetrigona*, *E*. *quadrangulata* (Michx.) Roem. & Schult., *E*. *robbinsii* Oakes, and *E*. *yecorensis* (all from the New World) probably represent a clade of closely related species. In light of this, the hypothesis is proposed that the origin and center of diversity of the *Eleocharis acutangula* complex is Neotropical. Since morphological data alone are probably insufficient for resolving the phylogeny of such closely related species within such a morphologically reduced genus, future studies using molecular markers will be necessary; but beyond the scope of this research.

CHAPTER VII

NOMENCLATURE

INTRODUCTION

The type method is an integral part of botanical nomenclature for it stabilizes a name (whether an accepted name or a synonym) by fixing it to a particular specimen, specimens, or other element examined by the original author. In cases where it is unclear which specimens were associated with the name by the author, or if the specimens are believed to be lost or destroyed, the *International Code of Botanical Nomenclature* (*ICBN*; Greuter et al. 2000) provides a method for selecting a lectotype or neotype. The *ICBN* places great emphasis on typification, thus, nomenclatural research comprises a substantial portion of systematic research. Although the nomenclature of all species treated in this research was reviewed, this chapter comprises discussion of noteworthy situations including clarification and letotypification. Decisions for or against lectotypification are discussed and defended in light of the *ICBN.* Suffice it to say that some nomenclatural uncertainties remain with some of the names studied, and more time will be required to resolve them.

A concept of nomenclatural types in the application of botanical names had its start in America with the Rochester Code of 1892, but did not become mandatory until the Paris Code of 1956 (Henry & Chandrabose 1980). Type specimens of names that predate the Rochester Code can be especially ambiguous. Only two names studied (*Eleocharis strobilacea* and *Heleocharis pseudofistulosa*) were published recently enough that the holotype had been explicitly designated. Research was necessary to determine the status of types for other names and if lectotypification or neotypification were necessary. In most cases, syntypes were readily available; in others, substantial correspondence with curators abroad was necessary to locate authentic specimens known to have been used by authors in describing new species. The only name for which a type was not directly examined was *E*. *mutata*. The “type” of *E*. *mutata* is a specimen known to have been nomenclaturaly associated with the protologue housed at the Linnaean Herbarium (LINN) in London. This specimen was too valuable to be loaned for study. However, high resolution photographs of the whole sheet and several achenes of this specimen were provided by LINN staff. In all, over ten previously unknown type specimens were discovered among general collections in the loans received for study.

NOMENCLATURAL HISTORY OF *ELEOCHARIS* SUBG. *LIMNOCHLOA*

Limnochloa, as first circumscribed by Lestiboudois (1819), comprised Robert Brown's (1810) species with three stigmas and trigonous achenes. Koyama (1961) chose *Eleocharis mutata* (which was among the original elements of Lestiboudois) to designate as type of *Limnochloa*, but incorrectly cited Nees von Esenbeck as author (Gonzáles-Elizondo and Peterson 1997). Egorova (1976) selected *E*. *quinqueflora* (Hartmann) O. Schwarz for a second type designation, a species neither among the original elements, nor even of the subgenus (Gonzáles-Elizondo and Peterson 1997). In an effort to stabilize the usage of *Limnochloa* at the rank of subgenus, Gonzáles-Elizondo and Peterson (1997) formally designated *E*. *mutata* as type. Although *E*. *mutata* never possesses trigonous achenes as was proposed in Lestiboudois' (1819) original description, Gonzáles-Elizondo and Peterson (1997) are still of the opinion that there is no reason it can not serve as type for *Limnochloa*, a position followed here since such ambiguities seem to be common in early nomenclatural systems in *Eleocharis*. Indeed, among Brown's (1810) original 20 species, only three have trigonous achenes, all of which now belong to subg. *Eleocharis* (Gonzáles-Elizondo and Peterson 1997).

NOMENCLATURAL HISTORY AND LECTOTYPIFICATION IN THE *ELEOCHARIS MUTATA* COMPLEX

Authorship and Typification of *Eleocharis mutata*

The *Eleocharis mutata* complex as treated herein comprises three species for which there are six published names available. *E*. *mutata* was first described under *Scirpus* by Elmgren (1759) a student of Linnaeus. Although Elmgren is sometimes cited as author (e.g., Svenson 1957; Haines & Lye 1983), the name was actually validly published later by Linnaeus (1759). As with most Linnaean names, the protologue provides no direct indication of any specimen upon which the name is based. This is not unexpected since the modern concepts and use of type specimens were unheard of prior to the last century (Henry & Chandrabose 1980). Römer & Schultes (1817) transferred the name to *Eleocharis*. Brown has sometimes been credited with authorship of *E*. *mutata*, but he merely indicated the correct placement of *S*. *mutatus* in his newly proposed genus *Eleocharis*. Subsequently, Nees von Esenbeck (1842) transferred the name to the genus *Limnochloa*.

Is there a need to lectotypify *Eleocharis mutata*? Browning et al. (1997) reported the “type” of *E*. *mutata* as being at LINN, but cited no specific specimen. This raises the issue as to if the name has been validly lectotypified according to current procedures outlined in the *ICBN*. Cafferty and Jarvis (2004) handled identical predicaments for several species of sedges by ascribing lectotype to a specific specimen. However, Mark Spencer (BM, pers. com.)

suggested that since there is only one specimen of *E*. *mutata* at LINN known to have been associated with Linnaeus (“71.2”), it seems prudent and conservative to accept the “typification” of Browning et al. (1997) for the time being. The inscription “mutatus” on the specimen was made by Linnaeus, and the plant fits his description.

Lectotypification of *Eleocharis spiralis*

Eleocharis spiralis was first described and illustrated under *Scirpus* by Rottböll based on plants sent to him by Koenig from India. The protologue designates no type, and the description is accompanied by a detailed illustration of a sterile specimen. Roemer & Schultes (1817) transferred the name to *Eleocharis* without indicating a type. Although Brown is sometimes recognized as author of this combination, as was the case with *E*. *mutata*, he merely indicated the correct placement of *S*. *spiralis* in *Eleocharis*. The Koenig Herbarium is housed at C, from which five specimens were received of *Eleocharis spiralis* collected by Koenig. Accession # L 56/2004 No 55 has traditionally thought to have been nomenclaturaly associated with the protologue of *Scirpus spiralis* Rottb. (Ib Friis, C, pers. comm.). It critically matches the various elements of the protologue and is herein designated as lectotype.

Lectotypification of *Eleocharis compacta*

Eleocharis compacta is based on *Brown 5934* from Australia. Upon Brown’s death in 1858, his personal herbarium was acquired by the British Museum, and duplicates were distributed to Kew, Edinburgh, Melbourne and

Sydney (Stearn 1960). Stearn (1960) suggested lectotypes for species described by Brown be sought at BM. Phototypes of two sheets of *Brown 5934* were received on request from BM and BM-000307758 is herein designated as lectotype. Two specimens of *Brown 5934* on loan from K are immature, but otherwise are referable to *E*. *spiralis*.

Confusion Surrounding *Eleocharis austro-caledonica*

Svenson (1929) treated *Eleocharis austro-caledonica* Vieill. (based on *Vieillard 1453*) as a synonym of *E*. *dulcis*, and then later under *E*. *spiralis* without explanation (Svenson 1939). Research has resolved the confusion surrounding *Vieillard 1453* and how *E*. *austro-caledonica* relates to *E*. *dulcis* and *E*. *spiralis*. A duplicate of *Vieillard 1453* was received on loan from BM. Photographs of three sheets of *Vieillard 1453* (one mixed with 1455) were also sent from P (where Vieillard's types are located). All of the specimens at P are annotated by Guillaumin as *E*. *dulcis*. On examination of the photographs the culms are conspicuously septate and spikelet characteristics agree with *E*. *dulcis*, not *E*. *spiralis*. However, the duplicate of *Vieillard 1453* from BM is immature, but is without a doubt *E spiralis*. Thus, evidently the elements of *E*. *austro-caledonica* comprise a mixed collection. It is currently not possible to determine to which elements Vieillard intended to apply the name, but since there are three specimens at P referable to *E*. *dulcis* and the protologue describes plants as a meter or more (probably too tall for *E*. *spiralis*), one must conclude it was meant for the specimens referable to *E*. *dulcis*.

NOMENCLATURAL HISTORY AND LECTOTYPIFICATION IN THE *ELEOCHARIS ACUTANGULA* COMPLEX

Lectotypification of *Eleocharis acutangula*

Undeniably the most tumultuous nomenclatural history of the taxa treated herein can be found in *Eleocharis acutangula*, mostly with regard to *Scirpus fistulosa* as described below. Other names associated with *E*. *acutangula* include *E*. *fistulosa* var. *robusta* and *E*. *planiculmis*. Multivariate analysis (see Chapter VI) has indicated that these are referable to *E*. *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. Indeed, for this species, an exhaustive literature search revealed no reference to any particular type specimen although a number of authors indicate a “type” from India (e.g., Haines & Lye 1983; Gordon-Gray 1995; Browning et al. 1997). Typifying Roxburgh names can be difficult since his collections 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 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 on both front and back by Roxburgh.

Queries were made to curators at key herbaria indicated by Forman (1997) in an effort to locate an authentic Roxburgh specimen. Mark Spencer (BM) found a specimen (BM-000847992) that he considers to be authentic, the most compelling evidence being annotations on the “verso” (back) and front of the specimen. The verso is annotated “Ind. Orient Roxburgh” in an unknown hand, indicating the specimen was received from Roxburgh, and the front was annotated “72” in what the author interprets to be Roxburgh’s hand. This specimen has been chosen as lectotype of *S*. *acutangulus* since it fits the description in the protologue and is known to have been used by Roxburgh.

Problems With Typification of *Scirpus medius*

Roxburgh also described *Scirpus medius* as being similar to *S*. *acutangulus* but having shorter culms with smooth, rounded angles. Nees von Esenbeck (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 *E*. *acutangula* examined during this research had triquetrous culms. No specimens annotated as *S*. *medius* were reviewed during this research, and no specimens were located in herbaria where Roxburgh’s specimens were distributed. For now, the opinion of Svenson (1929), and others (Blake 1939; Koyama 1985; Gordon-Gray 1995) is followed 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* Forssk. *Eleocharis fistulosa* Link is also invalid because Link failed to associate the final epithet with the name of the genus or species, or with its abbreviation, as mandated by the Art. 33.1 of the *ICBN* (Greuter et al. 2000). 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.

Lectotypificaton of *Eleocharis fistulosa* var. *robusta*

Eleocharis fistulosa var. *robusta* was 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 isolectotypes.

CHAPTER VIII

TAXONOMIC TREATMENT

DESCRIPTION OF *ELEOCHARIS* SUBG. *LIMNOCHLOA* WITH KEY AND SPECIES ACCOUNTS FOR TAXA TREATED

Eleocharis subg. *Limnochloa* (P. Beauv. *ex* T. Lestib.) Torr. (In Part)

Limnochloa P. Beauv. *ex* T. Lestib. Essai Cypér. 41. 1819. *Eleocharis* subg. *Limnochloa* (P. Beauv. *ex* T. Lestib.) Torr. Ann. Lyceum Nat. Hist. New York, 3: 296. 1836. *Eleocharis* sect. *Limnochloa* (P. Beauv. *ex* T. Lestib.) Benth. & Hook. F., Gen. Pl. 3: 1047. 1883. *Eleocharis* ser. *Mutatae* Svenson. Rhodora 31:127. 1929. *Eleocharis* sect. *Mutatae* (Svenson) T. V. Egorva & N. K. Khoi. Novosti Sist. Vyssh. Nizsh. Rast. 17:60. 1980. TYPE: *Eleocharis mutata* (L.) Roem. & Schult. (designated by González-Elizondo & Peterson 1997).

Plants perennial, aquatic, roots fibrous, sometimes with tubers, rhizomes creeping. Culms spongy with incomplete transverse septa, terete- triquetrous. Spikelets cylindric, terete, often as wide as culms; proximal scales empty or subtending a flower; floral scales spirally arranged, with obscure to prominent raised longitudinal veins adaxially, cartilaginous to indurate, distal margin 0.1-0.5 mm, hyaline-erose. Styles 3-fid. Achenes biconvex, distally abruptly constricted into a distinct neck or gradually tapering into an annular thickening or prolonged beak, markedly (to faintly) sculptured, usually with 11-22 longitudinal rows of polygonal cells. Tubercles distinct from achenes in color, texture and form, or sometimes merging with achene apex, often greatly dorsoventrally compressed.

Notes for Using Key and Species Descriptions

Specimens to be identified with reliability must possess mature achenes. Choices should be made following examination of several achenes. Achenes are fully mature when floral scales are disarticulated at the base from the rachilla and shed easily. Achene lengths do not include the tubercle; achene body length is measured from the point of attachment to the point of constriction at the summit. Triquetrous culms often fold flat when pressed and thus can appear terete. Characters that distinguish the *Eleocharis mutata* complex from the *E. acutangula* complex are indicated in the key.

Key for Identification of Members of the *Eleocharis mutata* and *E. acutangula* Complexes

1. Floral scales finely many veined (raised veins not clearly discernable at 20×); wing-like remnants on rachilla joints absent (torn edges of floral scales sometimes persisting); achene apex slightly constricted at the summit into a hard annular thickening or gradually narrowed into a stout spongy region of the same texture and color as the achene; apex of distal leaf sheath usually prolonged into an awn to 6 mm long (*E. mutata* complex)

2. Culms triquetrous to trigonous (rarely obscurely 3-angled or terete) distally; floral scales (2.3-)2.8-4 (-4.8) mm long; achene apex slightly constricted at the summit into a hard annular thickening; perianth bristles retrorsely spinulose (sometimes smooth in *E*. *spiralis*)
    3. Achene body (1.2-)1.3-1.6 (-1.9) mm long with ca. 20 longitudinal rows of transversely oblong cells; perianth bristles course-retrorsely spinulose, most exceeding the tubercle; floral scales ovate to broadly ovate, apex broadly rounded; distribution New World tropics and introduced to Africa ………...................…………..................... *E*. *mutata*
    3. Achene body (1.2-)1.3-2.1 mm long with ca. 17 longitudinal rows of transversely linear cells; perianth bristles irregularly spinulose or sometimes smooth, usually few surpassing the summit of the achene body; floral scales obovate to very widely obovate, apex truncate to broadly rounded; distribution Oceania and SE Asia, reportedly introduced to Madagascar …….…………………………….…… *E*. *spiralis*
2. Culms more or less terete or obscurely 3-angled distally (never triquetrous); floral scales (3.6-)4.2-4.9 (-5.3) mm long; achene apex gradually narrowed into a stout spongy region; perianth bristles usually smooth or rarely finely to coarsely retrorsely spinulose .... *E*. *cellulosa*

1. Floral scales coarsely many veined (raised veins clearly discernable at 20×); wing-like remnants on rachilla joints present (not to be confused with torn edges of floral scales); achene apex markedly constricted to a short neck, neck sometimes obscured by the style base; apex of distal leaf sheath not prolonged into an awn (*E*. *acutangula* complex)
    4. Culms more or less terete or distally obscurely 3-5-angled, never triquetrous; centrally located epidermal cells of achene transversely reniform ……...…………………..……………..………………….. *E*. *obtusetrigona*
    4. Culms triquetrous (rarely trigonous), never terete; centrally located epidermal cells of achene transversely oblong
        5. Longest perianth bristle 3.2-4 mm long, coarsely retrorsely spinulose nearly to the base; neck constricted 0.6-0.7 times achene width; tubercle 0.4-0.6 times long as wide ……………….…… *E*. *neotropica*
        5. Longest perianth bristle 3.2 mm long or shorter, the spinules retrorse, spreading, or sometimes absent; neck constricted 0.6 times achene width or less; tubercle 0.5-1.1 times long as wide
            6. Achenes with 18-22 longitudinal rows of cells on achene face; perianth bristles shorter than achene body, spinules mostly spreading; tubercle 0.7-0.9 mm long ………………..…. *E*. *steinbachii*

6. Achenes with usually 15 or fewer longitudinal rows of cells on achene face; perianth bristles shorter or longer than achene body, spinules mostly retrorse or seldom absent; tubercle 0.8 mm or less long
    7. Perianth bristles shorter than achene body (rarely few to all reaching its summit or slightly surpassing it) with few short, salient retrorse spinules near tips or less often restricted to distal half; achene body 1.4-1.7 mm long; tubercle 0.3-0.5 mm long ..……………..………………. *E. acutangula* subsp. *breviseta*
    7. Perianth bristles longer than achene body (rarely one to few just reaching its summit or slightly shorter) with coarsely retrorse spinules nearly to base or less often spinules absent; achene body 1.6-2 mm long; tubercle 0.5-0.8 mm long ………………… …………………………………. *E. acutangula* subsp. *acutangula*

***Eleocharis cellulosa* Torr. (Fig. 35 A-G)**

Eleocharis cellulosa Torr. Ann. Lyceum. Nat. Hist. New York, 3: 298. 1836. TYPE: U.S.A., Mississippi, Bay of St. Louis, wet sandy marshes, 1834, *Ingalls s.n.* (HOLOTYPE: NY!; ISOTYPE: GH!).

Scirpus dictyospermus Wright in Sauv. Fl. Cub. 175. 1873. TYPE: CUBA, En sabanas anegadizas, P. del Rio, *Wright 3763* (HOLOTYPE: GH!; ISOTYPES: K!, NY! [2-sheets], P!).

Plants perennial. Roots coarse, fibrous, dark gray-brown to maroon, tubers rarely seen; rhizomes long, 1-4 mm thick, scales to 6 mm long. **Fertile culms** terete or rarely obscurely 3 angled to sub-trigonous distally when emergent, (39-)46-81 (-97) cm tall × (0.9-)1.4-2.7 (-3.5) mm wide, soft to hard, internally spongy, with incomplete transverse septa, longitudinally striate when dry, shinny and smooth when fresh, light green. **Leaves** 2, reduced to sheaths, apically oblique, apex acute to acuminate, membranous, loose, friable, maroon-chestnut to cinnamon (orangeish) basally, brownish distally, apex of upper sheath usually extended into an awn to 6 mm long. **Spikelets** cylindric, obtuse, proximal (1-)2-9 (-10) scales empty, first scale amplexicaul and appearing as continuation of culm, (13-)24.4-43 (-52) mm long × (2.5-) 3.5-4.6 (-5.5) mm wide; floral scales appressed to loosely ascending upon drying, ovate to broadly ovate, apex broadly rounded, distal 0.1-0.4 mm hyaline-erose, central area broadly keeled from base to near middle, (3.6-)4.2-4.9 (-5.3) mm long × (2.2-)2.8-3.5 (-4) mm wide, finely many veined, mid-vein evident only in adaxial view, centrally indurate, stramineous, adaxially sparsely to densely red-maculate, abaxially sparsely red-maculate with a dark reddish-brown band near apex. **Flowers** with (5-)6-7 (-8) perianth bristles; bristles straight-tortuous, narrow to somewhat broad and strap-shaped proximally (rarely a bristle present abaxially that is variously forked only near the tip to nearly to the base), smooth or infrequently minutely nodulose (dark brown nodules seen only at high magnification), or bristles retrorsely spinulose nearly to base in some Caribbean plants, bristles 0.6-1.4 times achene body length, stramineous, spinules when present colorless, 0.03-0.08 mm long; stamens 3; anthers 1.4-2.0 mm long, yellow to reddish-brown; style 3-fid. **Achene** biconvex, more or less obpyriform, obovate to very widely obovate, the apex constricted to about 0.6 times achene width, broadening again into spongy beak of same texture and color as the achene, (1.5-)1.6-2.0 (-2.3) mm long × (1.2-)1.4-1.6 (-1.8) mm wide, with ca. (13-)16-19 (-23) longitudinal rows of deeply pitted transversely oblong cells visible through transparent periclinal layer on each achene face, dull, cream colored, maturing to lustrous amber or occasionally light brown; beak usually tapering apically or sometimes the central region spongy and the sides compressed (rarely appearing annulate as in *E*. *mutata*), (0.2-)0.4-0.8 (-1.1) mm high; tubercle usually distinct at high magnification or sometimes so gradually merging with beak as to be scarcely distinguishable from it, (0.1-)0.2-0.4 (-0.6) mm tall, dark brown.

Phenology and Ecology — Flowering from early June through early November in the SE United States. In the tropics, *Eleocharis cellulosa* probably flowers year round. In the SE United States forming extensive stands in wetlands of the coastal plain, and particularly near the coast although a few records occur from inland sites in Texas (the Edwards Plateau) and southern Arkansas. *Eleocharis cellulosa* is a dominant species of some wet-prairie vegetation types in the Florida Everglades (Loveless 1959). In the Caribbean, occurs in mangrove swamps, fresh to salty marshes, and other coastal wetland habitats.

Distribution — In North America north of México, currently known from Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, and Texas. In México from the states of Campeche, Nayarit, Nuevo Leon, Quintana Roo, Tabasco, Tamaulipas, and Yucatan. In Central America from Guatemala, Belize, Honduras, and Nicaragua. Also recorded from Bermuda. Widespread in the Caribbean Basin with records from Bahama Archipelago, Cuba, Cayman Islands (Proctor 1984), Jamaica, Haiti, Dominican Republic, and Puerto Rico. In South America known only from Venezuela.

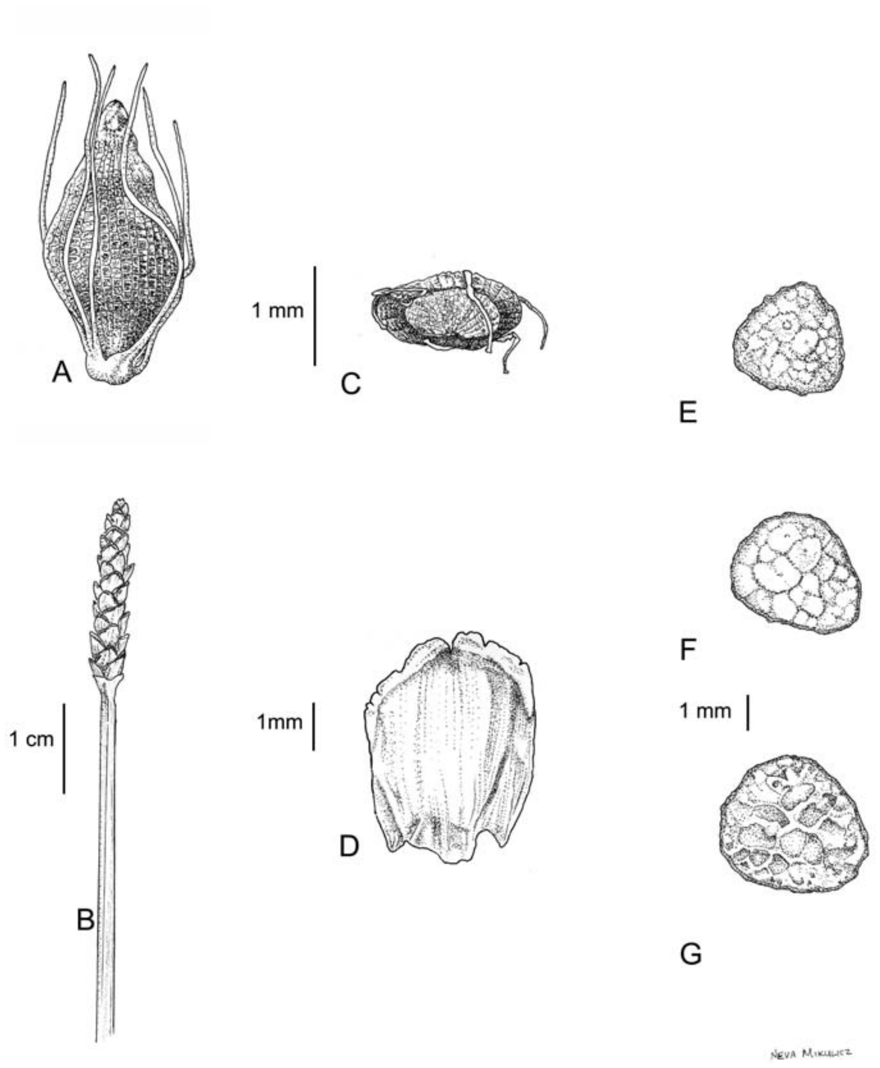


Fig. 35. Illustration of *Eleocharis cellulosa.* A. Detail of achene and perianth bristles. B. Spikelet and distal end of culm. C. Cross section of achene. d. Floral scale. E. Cross section of culm below spikelet. F. Cross section of culm 10 cm below spikelet. G. Cross section of culm above distal leaf sheath. A–C drawn from *Rosen 2968* (SBSC) and D-G drawn from *Rosen & Combs 3018* (TAES).

Eleocharis mutata **(L.) Roem. & Schult. (Fig. 36 A-G)**

Scirpus mutatus L., Syst. Nat. (ed. 10) 2: 867. 1759. *Eleocharis mutata* (L.) Roem. & Schult., Sys. Veg. 2: 155. 1817. *Limnochloa mutata* (L.) Nees, Fl. Bras. 2(1): 101. 1842. TYPE: JAMAICA (LECTOTYPE: LINN photo!).

Eleocharis scariosa Steud., Syn. Pl. Cyp. 80. 1855. TYPE: BRASIL, Sebastiana, Martius Herb. Fl. Bras. *Unknown 229* (HOLOTYPE: P; ISOTYPES: E!, GH!, M [2-sheets]!, MO!, NY!).

Plants perennial. Roots coarse, fibrous, gray-brown to maroon, tubers rarely seen; rhizomes long, 2-5 mm thick, scales to 8 mm long. **Fertile culms** triquetrous to trigonous, usually conspicuously so distally (rarely obscurely 3 angled to terete), sometimes twisted in plants growing in desiccated wetlands, (31-)53.8-93 (-116) cm tall × (2.2-)2.6-5.1 (-8.5) mm wide, soft to hard, internally spongy, with incomplete transverse septa, longitudinally striate when dry, shinny and smooth when fresh, dark green. **Leaves** 2, reduced to sheaths, apically oblique, apex acute to acuminate, membranous, loose, friable, maroon-chestnut to cinnamon brown, apex of upper sheath usually extended into an awn to 5 mm long. **Spikelets** cylindric, obtuse (acute), at least proximal 2-3 (-4) scales empty, first scale amplexicaul and appearing as a continuation of the culm, (12-)23-44 (-66) mm long × (3-) 3.8-5.4 (-8) mm wide; floral scales appressed to weakly spreading upon drying, ovate to broadly ovate, apex broadly rounded, distal 0.2-0.3 mm hyaline-erose, central area broadly keeled from base for ca. 1/3-1/2 scale length, (2.8-) 3.2-4 (-4.8) mm long × (1.9-) 2.5-3.4 (-4.8) mm wide, finely many veined (raised veins not conspicuous at 20×), mid-vein evident only in adaxial view, indurate, stramineous, abaxially red-maculate or more frequently with a dark band near apex, adaxially red-maculate. **Flowers** with (5-)6-8 perianth bristles; bristles straight-tortuous, narrow to somewhat broad and strap-shaped proximally, retrorsely spinulose nearly to the base, mostly exceeding achene, stramineous, margins and spinules sometimes dark reddish; stamens 3; anthers 1.3-2.0 mm long, reddish-brown; style 3-fid. **Achenes** biconvex, more or less obpyriform, obovate, or sometimes broadly elliptic, the apex constricted to about 0.6 times achene width, broadening again into hard annulus of same texture and color as the achene, (1.2-)1.3-1.6 (-1.9) mm long (not including annulus or tubercle) × (1-)1.1-1.4 (-1.8) mm wide, with ca. 20 longitudinal rows of deeply pitted transversely oblong cells visible through transparent periclinal layer on each achene face, dull, cream colored, maturing to lustrous olive-yellow (amber); annulus transversely oblong and sometimes tapering apically, transversely rhombic when viewed distally, (0.05-)0.09-0.18 (-0.3) mm high; tubercle dorsoventrally compressed, triangular (very shallowly triangular), well formed to withered, distinct or sometimes appearing to merge with annulus or shouldered by it, (0.15-)0.3-0.5 (-0.9) mm × 0.4-0.8 mm, dark brown.

Phenology and Ecology — Flowering year round and occurring in openings in mangrove swamps, fresh to salty marshes, brackish lagoons and inlets, inter-dune ponds, riverine wetlands, wet clear-cuts, and other coastal wetland habitats reportedly from 0 -1200 m. Reported as a forage and fiber crop and rice field weed by Simpson & Inglis (2001) and observed as forage for horses and cattle in southern Mexico (Rosen, pers. obs. 2006). Dried culms used for pack-saddle pads and sleeping mats in Galapagos Archipelago (Stewart 1911).

Distribution — In the United States known only from southeastern Texas. In México from Campeche, Chiapas, Coahuila, Colima (Revillagigedo Islands), Guerrero, Jalisco, Quintana Roo, Tabasco, Tamaulipas, Veracruz, and Yucatan. In Central America from Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, and Clipperton Island. In the Caribbean Basin known from Bahama Archipelago, Cuba, Cayman Islands, Jamaica, Haiti, Dominican Republic, Puerto Rico, Virgin Islands, Leeward Islands, Windward Islands, and southern Netherlands Antilles. In South America known from Brazil, Colombia, Ecuador (including the Galápagos Archipelago), French Guiana, Guyana, Paraguay, Surinam, Tobago, Trinidad, and Venezuela. In Tropical Africa from Angola, Congo, Liberia, Pemba, Senegal, Sierra Leone, South Africa, and Togo. Some Puerto Rican specimens [*Alain et al. 33006* (NY); *Proctor 42687* (US); and *Woodbury s.n.* (NY)] with perianth bristles thin and spinulose only near the tips and the culms terete may be contaminated with *E*. *cellulosa*.

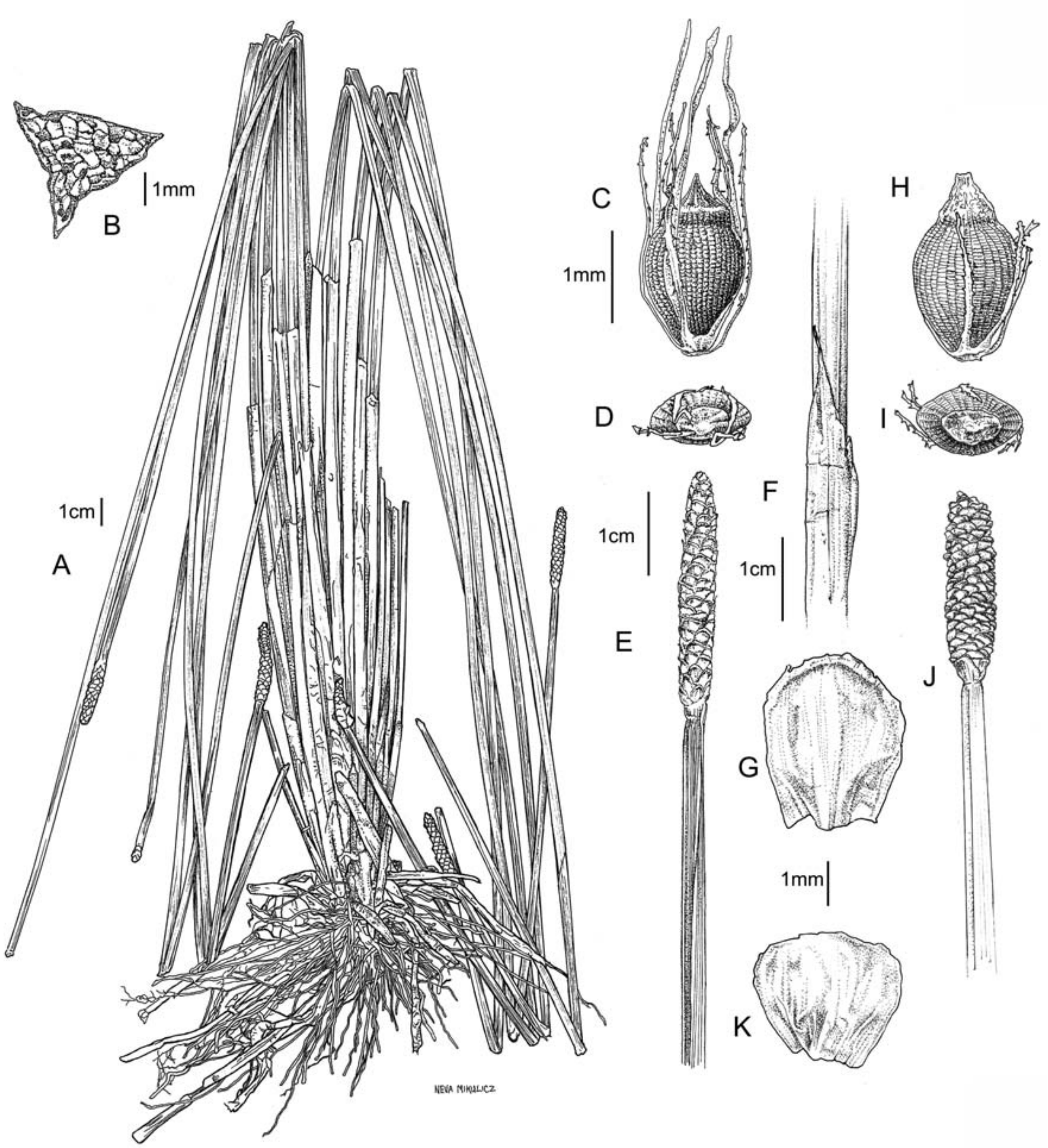


Fig. 36. Illustration of *Eleocharis mutata* and *E*. *spiralis*. A-G, *E*. *mutata*. A. Habit. B. Cross section at distal end of culm below spikelet. C. Detail of achene and perianth bristles. D. Cross section of achene. E. Spikelet and distal end of culm. F. Detail of apex of upper sheath. G. Floral scale. H-K, *E*. *spiralis*. H. Detail of achene and perianth bristles. I. Cross section of achene. J. Spikelet and distal end of culm. K. Floral scale. A-G drawn from *Rosen 2614* (MICH) and H-K drawn from *Clemens 9716* (K).

***Eleocharis spiralis* (Rottb.) Roem. & Schult. (Fig. 36 H-K)**

Scirpus spiralis Rottb., Descr. Icon. Rar. Pl. 45, t. 15, f. 1. 1773. *Eleocharis spiralis* (Rottb.) Roem. & Schult., Sys. Veg. 2: 155. 1817. *Limnochloa spiralis* (Rottb.) Nees. Contr. Bot. India. 114. 1834. TYPE: INDIA, Malabaria, *Koenig s.n.* (LECTOTYPE here designated: C [L 56/2004 No 55]!; ISOLECTOTYPES: C-4 sheets [L 56/2004 No 51-54]!).

Eleocharis compacta R. Br. Prodr. Fl. Nov. Holland. 224. 1810. *Scirpus compactus* (R. Br.) Spreng. Sys. Veg. 1. 1824. TYPE: AUSTRALIA, Northern Territory, Caledon Bay (Arnhem South Bay), Feb 1803, *Brown 5934* (LECTOTYPE here designated: BM [BM000901114] photo!; ISOLECTOTYPES: BM [BM000901117] photo!, K [K000307757, K000307758]!).

Eleocharis austro-caledonica auct. *non* Vieillard 1862; Svenson. Rhodora 41:11. 1939.

Plants perennial. Roots coarse, fibrous, gray-brown, tubers absent; rhizomes long, 2-3 mm thick, scales to 7 mm long. **Fertile culms** trigonous to nearly triquetrous, conspicuously so to near base in some specimens, or only distally or sometimes obtusely trigonous to terete, coarse, (29-)43.9-71 (-91.5) cm long × (1.4-)1.8-2.8 (-3.6) mm wide, soft to hard, internally spongy, with incomplete transverse septa, longitudinally striate when dry. **Leaves** 2, reduced to sheaths, apically oblique, apex acute to acuminate, membranous, loose, friable, often conspicuously and variably blotched from maroon, pink, to cinnamon brown, apex of upper sheath usually extended into an awn to 6 mm long. **Spikelets** cylindric, obtuse (acute), proximal 2-3 scales empty, first scale obtuse, amplexicaul, appearing as continuation of culm, (11-)18.7-32.6 (-41) mm long × (3-)3.8-5.2 (-6) mm wide; floral scales appressed, obovate to very widely obovate, apex truncate to broadly rounded, distal 0.2-0.3 mm hyaline-erose, central area distinctly broadly keeled from base to near middle, (2.3-)2.8-3.8 (-4.2) mm long × (2.0-) 2.4-3.3 (-3.7) mm wide, very finely many veined (raised veins not conspicuous at 20×), mid-vein evident only in adaxial view, a central obtriangular region indurate, cartilaginous to hyaline along sides, stramineous, scarcely abaxially red-maculate and sometimes with a dark band near apex, conspicuously adaxially red-maculate. **Flowers** with (4-)5-7 (-8) perianth bristles; bristles straight-tortuous, narrow, irregularly spinulose to smooth, usually half or fewer exceeding achene summit, stramineous, margins and spinules sometimes dark reddish; stamens 3; anthers (1.1-)1.3-1.7 (-1.8) mm long, reddish-brown; style 3-fid. **Achenes** biconvex or with (abaxial?) central bulge, obovate, or sometimes broadly obovate, apex constricted to about 0.6 times achene width, broadening again into hard annulus of same texture and color as achene, (1.2-)1.3-2.1 mm long × (0.93-)1.04-1.3 (-1.4) mm wide, with ca. 17 longitudinal rows of transversely linear cells with inconspicuous longitudinal interstitial ridges visible through transparent periclinal layer on each achene face, dull buff or cream colored, maturing through amber to lustrous dark brown; annulus narrowly oblong (indistinct) or prolonged and tapered, merging into a short conical tubercle, sometimes very similar in aspect to *E*. *cellulosa*, 0.1-0.2 (-0.3) mm high; tubercle dorsoventrally compressed, triangular, well formed to withered, distinct or sometimes appearing to merge with prolonged and tapered annulus, (0.3-)0.4-0.6 (-0.7) mm long × (0.4-)0.5 - 0.6 (-0.8) mm wide, dark brown.

Phenology and Ecology — Eleocharis spiralis flowers year round and occurs usually at low elevations in extensive stands on clayey to peaty soils in *Melaleuca* and mangrove swamps, saline flats, brackish to saline marshes, riverine wetlands, and other coastal wetland habitats (Cowie et al. 2000). In Indramaju, Java, reportedly used for making mats (Kern 1974).

Distribution — In Southeast Asia, known from China, India, Malaysia, Philippines, Sri Lanka, Thailand, and Vietnam. In Oceania known from tropical and subtropical regions of Australia (Northern Territory and Queensland), New Caledonia, and Papua-New Guinea. In Africa known from the Island of Mauritius and reported by Svenson (1939) from Madagascar.

Eleocharis acutangula (Roxb.) Schult. subsp. _acutangula_ (Fig. 37 A-B)

Scirpus acutangulus Roxb. Fl. Ind. 1: 216. 1820. *Eleocharis acutangula* (Roxb.) Schult. Mant. 2: 91. 1824. *Limnochloa acutangula* (Roxb.) Nees. Contr. Bot. India 114. 1834. TYPE: INDIA, *Roxburgh s.n.* (LECTOTYPE here designated: BM [BM000847992]!).

Scirpus medius Roxb. Fl. Ind. 1: 216. 1820. *Limnochloa media* (Roxb.) Nees. Contr. Bot. India 114. 1834. TYPE: INDIA, *Roxburgh s.n.* (not found).

Scirpus fistulosus Poir. Encyclopédie Méthodique, Botanique 6: 749. 1804. nom. illeg., non *Scirpus fistulosus* Forssk. 1775. *Eleocharis fistulosa* Link. Jahrbücher der Gewächskunde 3: 78. comb. inval. 1820. *Eleocharis fistulosa* Schult. Mant. 2: 89. 1824. TYPE: MADAGASCAR, *Poiret s.n.* (HOLOTYPE: P [Herbier du Petit-Thouars., P00376392]!; ISOTYPE: Herb. Poiret in Herb. Moquin-Tandon [P00370140]!).

Eleocharis fistulosa Schult. var. *robusta* Boeck. Flora lxii (62): 563. 1876. *Heleocharis robusta* (Boeck.) H. Hess. Ber. Schweiz. Bot. Ges. lxiii. 331. 1953. cum descr. ampl. TYPE: AFRICA, Africa centralis, Seriba Ghassas, in Lande der Djur ges, 1 Sep 1869, *Schweinfurth 2326* (LECTOTYPE here designated: GH!; ISOLECTOTYPES: Z [000006263, 000006265]!).

Eleocharis planiculmis Steud. Syn. Pl. Glumac. 2: 80. 1855. TYPE: JAVA, *Zollinger 281* (HOLOTYPE: P [P00368895]!; ISOTYPES: P [P00368896, P00368897]!, K [K000290950, K000290949]!).

Plants perennial. Roots coarse, fibrous, drab-brown to reddish; rhizomes elongated, to 1-4 mm thick, scales to 10 mm long (few seen). **Fertile culms** triquetrous (a few collections from Madagascar trigonous-obtusely trigonous) distally, (25-)37.8-80 (-135) cm long × (1.2-)2-4.4 (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, narrowly-lanceolate, (11-)21-39 (-56) mm long × (2.5-)3.2-4.8 (-6) mm wide, acute; proximal scale fertile, obtuse, amplexicaul-clasping, appearing as continuation of culm, remaining floral scales conspicuously spirally arranged, appressed to somewhat spreading at maturity, ovate-oblong, (2.5-)3.8-5.2 (-6) mm long × (1.7-)2.2-3.4 (-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), distal 0.1-0.5 mm hyaline-erose, central area nearly flat, coarsely many veined. **Flowers** with 6-7 perianth bristles; bristles sub-equal, usually 1.1-1.7 times achene body length (rarely one to 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 widely obovate to obovate, 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 0.4 times achene width; tubercle dorsoventrally compressed, shallowly triangular-deltate (triangular), 0.5-0.8 (-1) mm long × (0.5-)0.6-0.9 (-1.2) mm wide, stramineous, maturing to dark brown.

Phenology and Ecology — Flowering and fruiting throughout the year and collected from various disturbed and natural freshwater herbaceous and forested wetlands including marshy open grasslands, coastal savannas, and tropical forests from sea level to 2300 m. Forms expansive stands on a variety of soil types and is usually associated with other aquatic plants. Weedy in rice and other crop rotations and aquatic habitats (Simpson & Inglis 2001). Used as a fiber crop in Borneo, Brazil, and Sumatra (Simpson & Inglis 2001).

Distribution — Pantropic; in México from Chiapas, Hidalgo, Jalisco, Nayarit, Tabasco, and Veracruz-Llave. In Central America known from Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica, and

Panama. In the Caribbean Basin known from Jamaica, Dominican Republic, Dominica, and Grenada. In South America known from Colombia, Ecuador, Venezuela, Guyana, Surinam, Brazil, Paraguay, and Argentena. Some previous reports of *E*. *acutangula* from the Galápagos Archipelago are based on misidentified specimens of *E*. *obtusetrigona* (Stewart 1911). Other reports were not verified (e.g., Jørgensen and León-Yánez 1999), and no authentic specimens of *E*. *acutangula* from the Galápagos Archipelago have been seen. Perhaps most widespread and occurring in a greater variety of habitats in tropical Africa, with records from Angola, Botswana, Burkina 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. Sporadically distributed in Asia and Oceania with records from China, India, Indonesia, Japan, Malaysia, Philippine Islands, Siam, Sri Lanka, Vietnam, Australia, and Papua-New Guinea.

Eleocharis acutangula subsp. *acutangula* is an extremely variable taxon, and as described here includes forms requiring additional systematic study. Of particular interest are plants seen from Madagascar (including the type of *E*. *fistulosa*) with obtusely trigonous culms.

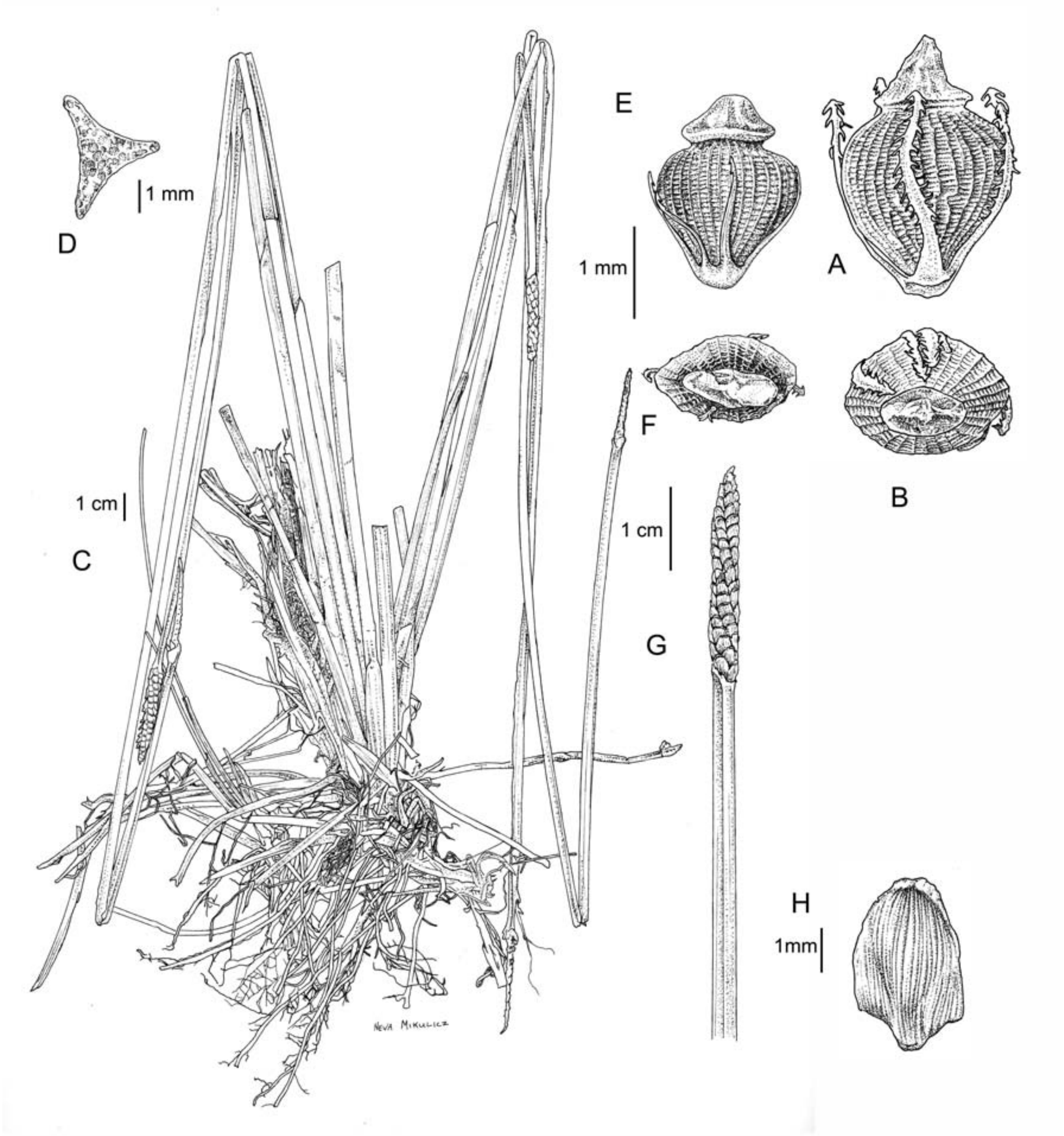


Fig. 37. Illustration of *Eleocharis acutangula* subsp. *acutangula* and *E*. *acutangula* subsp. *breviseta*. A-B, *E*. *acutangula* subsp. *acutangula*. A. Detail of achene and perianth bristles. B. Cross section of achene. C-H, *E*. *acutangula* subsp. *breviseta*. C. Habit. D. Cross section of culm below spikelet. E. Detail of achene and perianth bristles. F. Cross section of achene. G. Spikelet and distal end of culm. H. Floral scale. A-B drawn from *Hooper & Gandhi 2373* (MO) and C-H drawn from *Rosen & Carter 3206* (MICH).

***Eleocharis acutangula* (Roxb.) Schult. subsp. *breviseta* D. J. Rosen, subsp. nov. (Fig. 37 C-H)**. TYPE: **DOMINICAN REPUBLIC, El Seibo Province,** roadside ditch near Seibo, vicinity of Higuey, 3-7 Nov 1946, *Howard & Howard 9862* (HOLOTYPE: GH!; ISOTYPES: NY-2 sheets!, P!, US!).

A *Eleocharis acutangula* (Roxb.) Schult. subsp. *acutangula* acheniis parvibus, perianthii setis brevioribus cum spinulis retrorsis paucis et brevibus prope apicia, stylopodiis parvibus quasi depressoribus recidit.

Plants perennial. Roots coarse, fibrous, mostly maroon (a few drab-brown), small tuberous storage structures present in Florida plants, cylindrical-reniform, white; primary rhizomes thick, hard, ascending, concealed by roots and persistent culm bases (occurring in carefully collected specimens); secondary rhizomes elongated, to 3 mm thick, scales to 9 mm long (few seen). **Fertile culms** triquetrous, (19-)30.4-71 (-133.5) cm long × (1.1-)1.5-3.6 (-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 distil portion disintegrating when submerged), proximally dark maroon, distally drab, apex acute. **Spikelets** cylindric, narrowly-lanceolate, (10-)17-34 (-49) mm long × (2.2-)2.7-4.2 (-5.5) mm wide, acute; proximal scale fertile, obtuse, amplexicaul-clasping, appearing as continuation of culm; remaining floral scales conspicuously spirally arranged, appressed to somewhat spreading at maturity, ovate-oblong, (3.1-)3.3-4.6 (-5.9) mm long × (1.4-)1.8-2.9 (-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 0.1-0.3 mm hyaline-erose, central area nearly flat, coarsely many veined. **Flowers** with 5-7 perianth bristles; bristles sub-equal, 0.6-0.9 times achene body length (rarely few to all bristles exceeding 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, widely obovate, the shoulders and sides near apex usually straight and forming an obtuse angle, (1.3-)1.4-1.7 (-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 polygonal cells visible through transparent periclinal layer on each achene face, dull yellow-green maturing through amber to shiny dark brown, apex constricted to distinct neck about 0.4 times achene width, sometimes achenes persistent after floral scales have shed giving spikelet 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.

Etymology — The subspecific epithet describes the short perianth bristles of this taxon.

Phenology and Ecology — Collections examined were in flower and fruit from nearly throughout the year. Collections examined are from various disturbed and natural freshwater wetlands including marshy open grasslands and tropical forests reportedly from 0 -1400 m. Collections made in southern Florida were from a seasonally flooded savanna dominated by exotic hardwoods.

Distribution — In North America north of México, currently known only from Lee County, Florida. In México from the states of Campeche, Chiapas, and Guerrero. 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. Presumably introduced in southern Africa with records from South Africa, Tanzania, and Zimbabwe. One specimen from Ghana is probably best annotated as *E*. *acutangula* aff. subsp. *breviseta*.

Eleocharis neotropica **D. J. Rosen, sp. nov. (Fig. 38 A-C)**. TYPE: PERU, Departamento de Loreto, Maynas, Iquitos, prolongacion Yavari, Versailles-Paina, open annually burned grassland, 23 Mar 1974, *McDaniel & Rimachi 18552* (HOLOTYPE: MO!; ISOTYPES: IBE [2 sheets photo!], NY!).

Eleocharis acutangula (Roxb.) Schult. affinis, a que imprimis differt perianthii setis grosse retrorsum spinulis 2x vel quasi longitudibus achenio, collum 0.6-0.7 x latitude achenio, stylopodio latitudiore quam longio.

Plants perennial. Roots coarse, fibrous, drab-brown; primary rhizomes thick, hard, ascending, concealed by roots and persistent culm bases, secondary rhizomes elongated, to 3.2 mm thick, scales to 14 mm long (few seen). **Fertile culms** triquetrous, (44-)56-86 (-106) cm long × (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, narrowly-lanceolate, (15-)20-31 (-35) mm long × (3-)3.2-4.2 (-4.5) mm wide, acute; proximal scale fertile, obtuse, clasping, appearing as 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), distal 0.2-0.3 mm hyaline-erose, central area nearly flat, abaxially coarsely many veined. **Flowers** with (5-)6-7 perianth bristles; bristles sub-equal, (1.8-)1.9-2.3 (-2.4) times achene body length, coarsely retrorsely spinulose nearly to the base, stramineous, sometimes becoming reddish-brown distally; stamens 3; anthers 0.9-1.8 (-2.3) mm long, stramineous; style 3-fid. **Achenes** biconvex, widely obovate, (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.

Etymology — The specific epithet indicates the decidedly neotropical distribution of this taxon.

Phenology and Ecology — Collections examined were in flower and fruit from nearly throughout the year. Apparently endemic to the western Amazon. Collections examined are from various freshwater wetlands including marshy open grasslands, tropical forests, and roadside ditches, reportedly from 0 -1000 m.

Distribution — Known only from northwest South America from Ecuador, Bolivia, and Peru.

Eleocharis neotropica is very closely related to *E*. *acutangula*, differing in its achenes which have perianth bristles coarsely retroresely spinulose and at least twice as long as the achene body, and a neck 0.5-0.6 times as wide as the achene. In the herbarium, the two are indistinguishable vegetatively, making the presence of mature achenes necessary for identification. Field studies could lead to discovery of important vegetative or ecological characters that could aid in identification.

Other specimens examined (Paratypes). **SOUTH AMERICA. ECUADOR: Provincia del Pastaza:** Villano, Compamento Base de Arco, Pantano al noreste de la pista, bosque humedo tropical, potrero sobre suelo aluvial, 1^{o} 29'S, 77^{o} 27' W, Feb 1994, *Palacios 12171* (CIIDIR, MO). **Provincia de Napo:** Archidona, Reserva Ecologica Antisana, Comunidad Shamato, Entrada por km 21, Shamato, growing in muddy area of cow pasture, 00^{o} 43'S, 077^{o} 49'W, 24 Apr 1998, *Clark et al. 5122* (MO). **PERU: Departamento de Amazonas:** Bagua, along roadside from Chiriaco to Puente Venezuela (3.9 Km NE Chiriaco), elev. 600-800 ft., in standing water, 31 Oct 1978, *Barbour 4355* (F, IBE photo, MO). **Departamento de Cusco:** Paucar Tawbo, Montaueza Choutachaca, 780-1000 m, 28 Nov 1965, *Vargas 16887* (US). **Departamento de Loreto:** Peurto Almendras on the Rio Nanay, 30 km N of Iquitos, 600 m, 16 Aug 1981, *Moore & Ruiz 114* (F); Prov. Maynas, hierba de 80 cm, con flores de coler crema triangulado "Piripiri", 03 Aug 1967, *Torres 340* (GH [2 sheets]); Prov. Maynas, Iquitos, Carretera de Zungaro Cocha, cerca a la quebrada de Shushuna, en terreno arenosos, monte abierto, elev. Ca 140 m+, "piripiri", fls. white, 12 Aug 1983, *Rimachi 6908* (IBE photo, VSC); Maynas, Dtto. Punchana, Rio Nanay, varadera de; caserio de Padre Cocha, en monte abierto, terreno lodoso, elev. Ca 100 m, piripiri, 07 Jul 1994, *Rimachi 11004* (IBE photo, MICH [2 sheets], NY, VSC); Maynas, Inmediaciones de la Guarnicion militar de Gueppi, sobre la margen izquierda del Rio Putumayo, borde con Ecuador, 26 May 1978, *Diaz 368* (F, MO); Maynas, Distrito Iquitos, Caserio Nina Rumy, Rio Nanay, Bosque secundario no inundable, 73° 25' W, 03° 48' S, 22 Apr 1988, *Ruiz 1262* (MO) ; Iquitos Region, growing in water, 26 Jul 1966, *Martin & Lau-Cam 1164* (GH). **Departamento de Huanuco:** Leoncio Prado, 3 km SE of Pucayacu, on road from Tingo Maria to Tocache Nuevo, ca 75 km NW of Tingo Maria, 10 Dec 1981, *Plowman & Rury 11288A* (MO, NY). **BOLIVIA: Departamento de Pando:** Provincia Nicolas Suarez, Cobija 2 km hacia el Sur, 19 Oct 1988, *Beck 17139* (K, US).

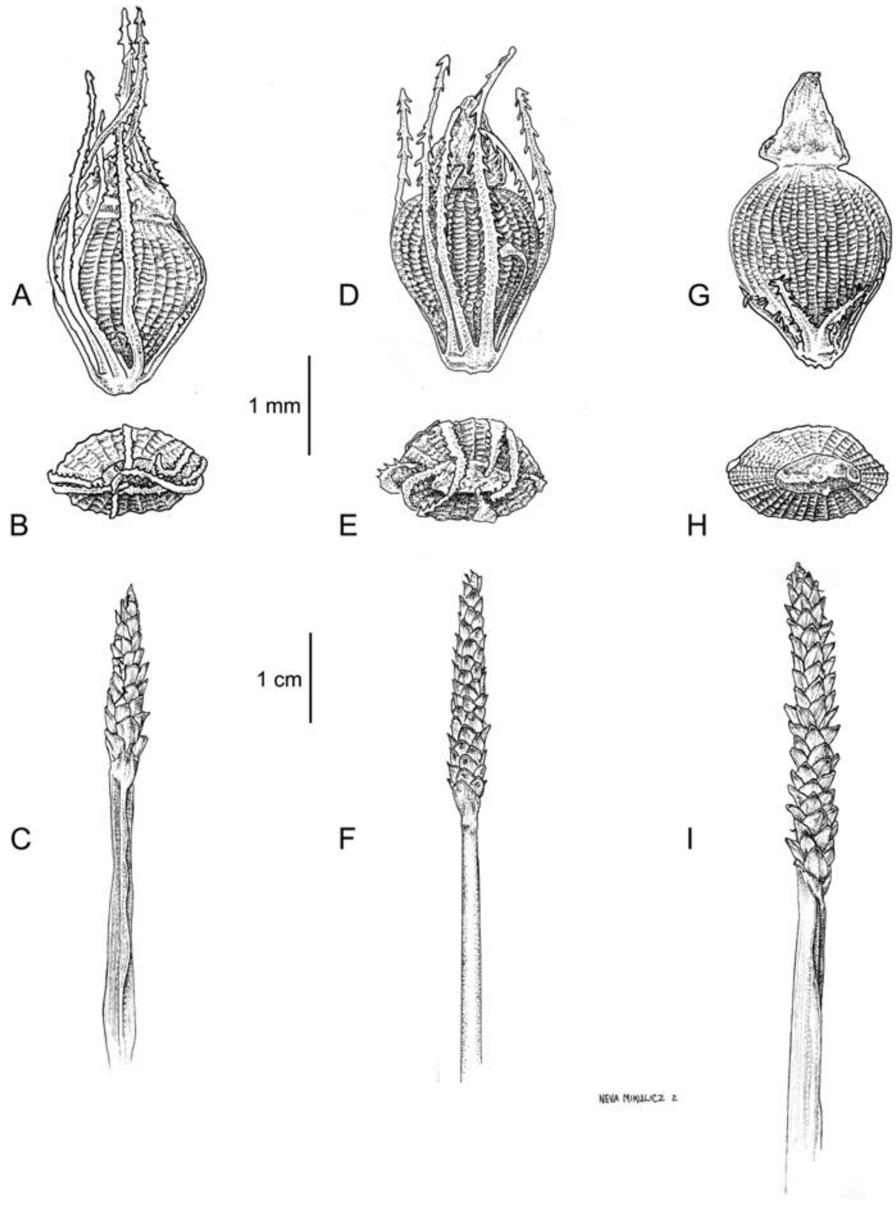


Fig. 38. Illustration of *Eleocharis neotropica*, *E*. *obtusetrigona*, and E. *steinbachii*. A-C, *E*. *neotropica*. A. Detail of achene and perianth bristles. B. Cross section of achene. C. Spikelet and distal end of culm. D-F, *E*. *obtusetrigona*. D. Detail of achene and perianth bristles. E. Cross section of achene. F. Spikelet and distal end of culm. G-I, *E*. *steinbachii*. G. Detail of achene and perianth bristles. H. Cross section of achene. I. Spikelet and distal end of culm. A-C Drawn from holotype, *McDaniel & Rimachi 18552* (MO); D-F drawn from *Pedersen 7634* (C); and G-I drawn from holotype, *Steinbach 7444* (GH).

***Eleocharis obtusetrigona* (Lindl. & Nees) Steud. (Fig. 38 D-F)**

Scirpus obtuse-trigonus Salzm., Herb. Lindley. *nom nud*. *Eleocharis obtusetrigona* (Lindl. & Nees) Steud. Syn. Pl. Glumac. 2: 80. 1855. *Limnochloa obtusetrigona* Lindl. & Nees. Fl. Bras. 2(1): 100. 1842. *Eleocharis mutata* (L.) Roem. & Schult. var. *obtusetrigona* (Lindl. & Nees) C.B. Clarke. Bull. Herb. Boissier 6 (Append. 1): 20. 1898. *Eleocharis fistulosa* (Poir.) Schult. var. *obtusetrigona* (Lindl. & Nees) Barros. Sellowia 12: 262. 1960. TYPE: BRASIL, Bahia, Martius, *Salzmann s.n.* (HOLOTYPE: CGE photo!; ISOTYPES: E!, MO!, P!).

Eleocharis strobilacea Pedersen. Darwiniana 12: 243, f. 1. 1961. TYPE: Argentina, Prov. Corrientes, Dep. Mburucuya, Estancia Santa Teresa, 21 Jan 1951, *Pedersen 957* (HOLOTYPE: C!; ISOTYPES: LP, [based on Pedersen’s designation of “Tipo” and “Isotipo”] GH!, NY!, US!).

Plants perennial. Roots coarse, fibrous, gray-brown, tubers absent; rhizomes elongated, (1.3-)1.5-3.5 (-4) mm thick, scales to 9 mm long (rarely seen in herbarium specimens). **Fertile culms** obscurely 3-angled to terete or rarely distinctly trigonous distally, (45.5-)50-82 (-90.2) cm long × (1.8-)2.4-5 (-6.2) mm wide, soft, internally spongy, with incomplete transverse septa, smooth, olive-gray (when dry). **Leaves** 2, reduced to sheaths, apically oblique, membranous, loose, friable, proximally dark maroon, distally cinnamon to orange-rufous, apex acute. **Spikelets** cylindric, narrowly-lanceolate, (19-)22.8-39 (-42) mm long × (3.7-)4-4.7 (-5) mm wide, acute, proximal scale fertile, obtuse, amplexicaul, appearing as continuation of culm, sometimes subtended by an annular swelling; floral scales appressed to weakly spreading, ovate-widely ovate, (4.7-)4.8-5.2 (-5.3) mm long × (2-)2.2-2.9 (-3.1) mm wide, cartilaginous, olive-gray centrally with a sub-apical dark splotch, stramineous marginally, abaxially and adaxially sparsely red-maculate, apex acute (rounded), distal 0.2-0.3 mm, hyaline erose, central area nearly flat, coarsely many-veined. **Flowers** with 6-8 perianth bristles; bristles sub-equal, mostly exceeding tubercle, ascending, broad and strap-shaped proximally, coarsely retrorsely spinulose nearly to the base, stramineous; stamens 3; anthers 1.7-2.2 (-2.4) mm long, reddish-brown; style (2-)3-fid or sometimes bifid. **Achenes** biconvex, more or less obpyriform to widely obovate, 1.7-2 (-2.1) mm long × 1.3-1.5 (-1.6) mm wide, with (11-)12-16 (-18) longitudinal rows of concave, transversely oblong polygonal cells that are (at least the most centrally located) transversely reniform, visible through transparent periclinal layer on each achene face, dull-buff, maturing to shiny dark green blotched with (or else entirely) amber, apex constricted to about 0.4 times achene width to a distinct neck (this sometimes obscured by style base); tubercle dorsoventrally compressed, deltate, (0.5-)0.6-0.9 (-1.1) mm long × (0.6-)0.7-0.9 (-1) mm wide, light to dark brown.

Phenology and Ecology — Flowering year round throughout its range. Scant label data of the specimens studied indicate *Eleocharis obtusetrigona* forms large stands in permanent shallow water and moist ground of a variety of freshwater wetland habitats from near sea level to ca. 1200 m.

Distribution — Known from a few localities in the United States (Texas) and Mexico (Veracruz). In Central America known from Guatemala, Honduras, El Salvador, Nicaragua and Costa Rica. In South America more widely distributed from Brazil, Paraguay, and Argentina. Recently, reported for the first time from the Galápagos Archipelago (Rosen & Hatch 2006). Probably once common in the Lower Rio Grande Valley of Texas where it now appears to be extirpated due to drainage of wetlands for development and agriculture. Thus, *Eleocharis obtusetrigona* might have ranged continuously from South America, through Central America and Mexico into southern Texas.

***Eleocharis steinbachii* D. J. Rosen, sp. nov. (Fig. 38 G-I)**. TYPE: BOLIVIA, Departamento de Santa Cruz, Lagunas pandas, Campos B.-Vista, Prov. Sara, 450 m, 24 Jan 1926, *Steinbach 7444* (HOLOTYPE: GH!; ISOTYPES: E!, F!, MO!, NY!, PH!, Z!).

Valde similis *E*. *acutangula* (Roxb.) Schult., sed differt acheniis, cum brevis rigidisque perianthii setis (interdum unifurcatis) cumque sparsis plerumque effusis spinulis et numerosioribus verticalibus seriebus epidermicarum cellularum.

Plants perennial. Roots coarse, fibrous, mostly drab-brown; rhizomes elongated, to 3.5 mm thick, scales to 8.6 mm long (few seen). **Fertile culms** triquetrous, especially distally, (56-)66.6-82.3 (-83) cm long × (4.2-)4.4-5.6 (-5.8) mm wide, soft, internally spongy, with incomplete transverse septa, smooth-finely longitudinally striate, grayish green when dry. **Leaves** 2 (-3), reduced to sheaths, apically oblique, membranous, loose, friable, proximally dark maroon, becoming chestnut to tawny distally, apex acute. **Spikelets** cylindric, narrowly-lanceolate, at least proximal 2-3 scales empty, first scale amplexicaul and appearing as continuation of culm, (37-)40-51 (-53) mm long × (5-)5.1-6 mm wide, acute; floral scales conspicuously spirally arranged, somewhat appressed to loose at maturity, ovate-widely ovate, 5.1-5.7 (-6) long × (3-)3.2-4 (-4.3) mm wide, cartilaginous, stramineous, adaxially red-maculate, apex obtuse (rounded), distal 0.2-0.3 mm hyaline-erose, central area nearly flat, coarsely many veined. **Flowers** with 6-7 perianth bristles; bristles unequal (some greatly reduced), stiff, short, 0.4-0.7 (-0.9) times achene body length, irregularly spinulose, the spinules mostly spreading (a few may be retrorse or antrorse), stramineous or sometimes colorless, usually with a conspicuously forked bristle adaxially; stamens 3; anthers (1.5-)1.9-2.6 mm long, reddish brown; style 3-fid. **Achenes** biconvex, widely ovate, 1.8-2.1 (-2.2) mm long × 1.4-1.6 (-1.7) mm wide, with (17-)18-22 longitudinal rows of concave transversely oblong polygonal cells visible through transparent periclinal layer on each achene face, dull, light brown splotched with amber maturing to cinnamon brown, apex constricted to a distinct neck about 0.5-0.6 times achene width; tubercle lameliform, deltate, 0.7-0.9 mm long × 0.8-0.9 (-1) mm wide, dark brown.

Etymology — This species is named in honor of José Steinbach, a German born natural history collector. Steinbach lived and worked in Argentina and Brazil in the late 1800s and early 1900s, collecting plants, vertebrates, and invertebrates and selling his collections to numerous individuals and institutions, most notably the Carnegie Museum.

Phenology and Ecology — Specimens were flowering and fruiting from November through January. Although ecological data on specimen labels are scant, it is presumed that *Eleocharis steinbachii* most likely inhabits various wetland habitats and is reported from savannas and seasonally wet forests from 200-500 m.

Distribution — Endemic to the Llanos de Mojos (Moxos) region of northern Bolivia in the southernmost portion of the Amazon Basin.

Eleocharis steinbachii is very closely related to *E*. *acutangula* differing in its ovate achenes which have short, stiff perianth bristles with spreading spinules and more numerous vertical rows of epidermal cells. In the herbarium, the two are indistinguishable vegetatively, making the presence of a mature achenes necessary for identification. Field studies could lead to discovery of important vegetative or ecological characters that could aid in identification.

Other specimens examined (Paratypes). **SOUTH AMERICA. BOLIVIA: Departamento del Beni:** Yacuma, Santa Borja 50 km hacia San Ignacio de Majos, Porvrnir-Estacion Biologica Beni 250 m, 27 Feb 1987, *Beck 13190* (NY); Ballivian, Estancia El Porvenir, 50 km E of the Rio Maniqui (San Borja) on the road to Trinidad, vicinity of Laguna Normandia, elev. 250 m., 14^{o}49'S, 66 ^{o}25'W, margin of lake, 17 Nov 1985, *Solomon 14766* (MO).

Excluded names and species not seen

It is worth mentioning *Eleocharis fistulosa* var. *micrantha* Chermezon described from specimens from Senegal (Chermezon 1936). Attempts to locate type specimens cited in the protologue have been unsuccessful thus far. Svenson (1939) relegated this name to synonymy under *E. nupeensis* Hutchinson & Dalziel based on the description, a temporary solution at best that is followed here.

Heleocharis pseudofistulosa H. Hess from Angola is based on *Hess 52/220* (Hess 1953). This specimen was not included in a loan of specimens received from Z and ZT. However, based on the description in the protologue, and an immature specimen of *Hess 52/525* (Z; a possible Isoparatype) annotated as *E*. *pseudofistulosa*, it is no different than *E*. *acutangula* subsp. *acutangula*. Svenson (1939) treated *Scirpus angulatus* Willd. *ex* Kunth as a synonym of *E*. *fistulosa*. No type specimens or specimens annotated as *S*. *angulatus* could be located.

CHAPTER IX

SUMMARY AND SUGGESTED FUTURE RESEARCH

Eleocharis subg. *Limnochloa* comprises species that are ecologically important (e.g., Loveless 1959; Palma-Silva et al. 2000; Rosen, pers. obs. 2002-2006), provide food, forage, and fiber crops for human use (Simpson & Inglis 2001), and as with other species of *Eleocharis* have great potential in ecological restoration and water pollution attenuation and abatement for human health and welfare (Fraser & Kindscher 2001). This research suggests that the subgenus is richer than previously reported and is in need of a worldwide revision. This research has also revealed that critical study of supposedly well defined species in *Eleocharis* subg. *Limnochloa* can result in range extensions, discovery of new taxa, and discovery of morphologically conservative characters that can aid in identification and provide insight into phylogenetic relationships.

Several problems investigated herewith need further study. However, morphometric numerical analysis may not be sufficient to resolve the taxonomy of some groups. The variability observed within *E*. *acutangula* subsp. *acutangula* and its relationship to *E*. *fistulosa*, and the variability between populations of *E*. *cellulosa* would be best tackled by employing molecular techniques, particularly those suitable for study of plant populations (Parker et al. 1998). Allozyme studies have been widely employed and proven useful to examine the genetic distance and elucidate the phylogeny of closely related and morphologically similar species of *Carex* (e.g., Ford et al. 1998). In several instances, isozyme data has supported and even bolstered systematic studies employing macro and micromorphological characters in *Carex* (e.g., Bruederle & Fairbrothers 1986; Ford et al. 1991). Parker et al. (1998) recommend the use of allozyme variation over nucleic acids when feasible, owing to the relatively inexpensive and straightforward nature of the former. However, In the last decade, numerous techniques utilizing DNA based markers have been developed that provide more variable and precise approaches for estimating genetic variance among individuals and between populations than protein based markers (Cruzan 1998). Allozymes might remain useful, but constraints such as low levels of polymorphism has brought about increasing interest in more informative DNA markers, particularly non-coding regions (Nybom 2004). Among the first and more commonly used markers were AFLPs (amplified fragment length polymorphisms), RAPDs (random amplified polymorphic DNA), RFLPs (restriction frasgment length polymorphisms), and VNTRs (variable number tandem repeats including microsatelites; Cruzan 1998; Nybom 2004)

A host of studies utilizing microsatelites have been published for a wide variety of angiosperms families, but only two were found for Cyperaceae. Blum et al. (2005) demonstrated the potential of microsatelites in the study of Cyperaceae by characterizing 16 microsatellite loci in *Schoenoplectus americanus* (Pers.) Volkart *ex* Schinz & R. Keller. Blum et al. (2005) found that most loci also amplified in a closely related species, *S. pungens* (Vahl) Palla, and that five loci exhibited species-specific alleles or distinct allelic size distributions to aid in discriminating *S*. *americanus* from *S*. *pungens*. Scotti et al. (2002) used AFLPs to confirm hybridization in the genus *Schoenus* L. in northern Italy.

No published studies utilizing molecular markers to elucidate the relationships of closely related species in *Eleocharis* were found. However, a few phylogenetic studies have been published for *Eleocharis*. Only one study investigating phylogeny at the subgeneric level in *Eleocharis* could be located in which González-Elizondo et al. (1997) used morphological characters to construct phenetic and cladistic classifications of *Eleocharis* subg. *Zinserlingia* T. V. Egorova sect. *Pauciflorae* Beauverd. The remaining phylogenetic studies published have focused on infrageneric revision utilizing molecular data. In these two recent studies, an *Eleocharis* subg. *Limnochloa* clade based on nuclear ribosomal ITS (internal transcribed spacer) sequences was well supported (Roalson & Friar 2000; Yano et al. 2004). However, in both studies only a limited number of species from subg. *Limnochloa* were included in the analyses which resulted in the pairing of taxa morphologically distinct. It has been suggested that species belonging to sect. *Pauciflorae* are the most primitive in *Eleocharis* (González-Elizondo et al. 1997). In studies by Roalson & Friar (2000) and Yano et al. (2004), subg. *Limnochloa* appears to be sister to a clade containing *Eleocharis* subg. *Zinserlingia* sect. *Pauciflorae* and an orphaned *E. tortilis* (Link) Schult., which suggests that these species would be an appropriate outgroup for phylogenetic analysis of subg. *Limnochloa*.

Morphometric analysis will be useful for defining species and addressing other problems in *Eleocharis* subg. *Limnochloa*, and could prove important as an aid in revision of what Svenson (1939) termed the slender South American species, comprising *E*. *elongata*, *E*. *mitrata* (Griseb.) C. B. Clarke, *E*. *jelskiana* Boeckl, and *E*. *plicarhachis* (Griseb.) Svenson. These taxa and their synonyms are all in need of critical review. Two well known species in temperate North America, *E*. *robbinsii* and *E*. *quadrangulata*, potentially include segregates in need of formal recognition (González-Elizondo 2002). Problems in Old World taxa are too numerous to list here. A preliminary review of specimens of *E*. *variegata* suggests this Old World species probably represents a complex of undescribed taxa. These problems will be approached in due course. The complex of species presented in this research will be revisited and evaluated using molecular analysis at some future date.

REFERENCES

BAKSH, S. I. and J. H. RICHARDS. 2006. An architectural model for *Eleocharis*: morphology and development of *Eleocharis cellulosa* (Cyperaceae). Amer. J. Bot. 93:707-715.

BARROS, M. 1928. Ciperaceas Argentinas. Anals Mus. Nac. Hist. Nat. Buenos Aires 34:425-496.

BARROS, M. 1960. Las ciperáceas del estado de Sant Catalina. Sellowia 12:262.

BEAUVERD, G. 1921. A propos d'une nouvelle espèce européenne du genre *Eleocharis*. Bulletin Societe Botanique de Geneve Series 2, 13:245-265.

BENTHAM, G. and J. D. HOOKER. 1883. Genera Plantarum Vol. 3, no. 2. Lovell Reeve & Co., London.

BLAKE, S. T. 1939. A monograph of the genus *Eleocharis* in Australia and New Zealand. Proc. Roy. Soc. Queensland 50:88-132.

BLASER, H. W. 1941. Studies in the morphology of the Cyperaceae. I. Morphology of flowers. A. Scirpoid genera. Amer. J. Bot. 28:542-551.

BLUM, M. J., J. S. MCLACHLAN, C. J. SAUNDERS, and J. D. HERRICK. 2005. Characterization of microsatellite loci in *Schoenoplectus americanus* (Cyperaceae). Mol. Ecol. Notes 5:661-663.

BÖCKELER, O. 1870. Die Cyperaceen des Königlichen Herbariums zu Berlin. Linnaea 36:385-512.

BREMER, K. 2002. Gondwanan evolution of the grass alliance of families (Poales). Evolution 56:1374-1387.

BRITTON, N. L. 1889. The genus *Eleocharis* in North America. Journ. N. Y. Micr. Soc. 4:95-111.

BRITTON, N. L. 1907. The sedges of Jamaica. Bull. Dept. Agr. Jamaica 5, Suppl. 1.

BROWN, R. 1810. Prodromus florae Novae Hollandiae. Hafner Pub. Co., New York.

BROWNING, J., K. D. GORDON-GRAY, and C. J. WARD. 1995. Cyperaceae, new records for Southern Africa and Kwazulu-Natal. Bothalia 25(2):238-239.

BROWNING, J., K. D. GORDON-GRAY, and C. J. WARD. 1997. Studies in Cyperaceae in Southern Africa 32: *Eleocharis* subgenus *Limnochloa* section *Limnochloa*. S. Afr. J. Bot. 63(4):172-184.

BRUEDERLE, L. P. and D. E. FAIRBROTHERS. 1986. Allozyme variation in populations of the *Carex crinita* complex (Cyperaceae). Syst. Bot. 11:583-594.

BRUHL, J. J. 1995. Sedge genera of the world: relationships and a new classification of the Cyperaceae. Aust. Syst. Bot. 8:125-305.

CAFFERTY, S. and C. E. JARVIS. 2004. Typification of Linnaean plant names in Cyperaceae. Taxon 53:177-181.

CATLING, P. M. and S. G. HAY. 1993. The hybrid origin of *Eleocharis macounii*. Rhodora 95:85-97.

CATLING, P. M. 1994. *Eleocharis compressa* x *Eleocharis erythropoda*, a new natural hybrid spike rush from Ontario. Can. J. Bot. 72:837-842.

CHERMEZON, H. 1936. Contribution à la flore cypérologique du Sénégal: Cypéracées récoltées par M. Trochain. Arch. Bot. Mem. 7:1-32.

CLARKE, C. B. 1898. Cyperaceae. In: R. Chodat, Plantae Hasslerianae soit énumération des plantes récoltées par le Dr. Émile Hassler, d'Aarau (Suisse) de 1885-1895 et déterminéespar le Prof. Dr. R. Chodat avec l'aide de plusiers collaborateurs. Bull. Herb. Boissier 6, Appendix 1:19-22.

CLARKE, C. B. 1900. Cyperaceae. In: I. Urban, ed. Symbolae Antillanae, Vol. 2. Fratres Borntraeger, Leipzig. Pp. 1-160.

CLARKE, C. B. 1902. Cyperaceae. In: W. T. Thiselton-Dyer, ed. Flora of Tropical Africa, Vol. 8. Ashford. Pp. 266-527.

CLARKE, C. B. 1908. New genera and species of Cyperaceae. Kew Bull. Add. Ser. 8:1-196.

COWIE, I. D., P. S. SHORT, and M. OSTERKAMP MADSEN. 2000. Floodplain flora: A flora of the coastal floodplains of the Northern Territory, Australia. ABRS, Canberra.

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

CRONQUIST, A. 1988. The evolution and classification of flowering plants., 2d ed. New York Botanical Garden, New York.

CRUZAN, N. B. 1998. Genetic markers in plant evolutionary ecology. Ecology 79:400-412.

DAGHILIAN, C. P. 1981. A review of the fossil record of monocotyledons. Bot. Rev. 47:517-555.

DAHLGREN, R. M. T. and F. N. RASMUSSEN. 1983. Monocotyledon evolution characters and phylogenetic estimation. In: M. K. Hecht, B. Wallace, and G. T. Prance, eds. Evolutionary biology, Vol. 16. Plenum Publishing Corporation, New York. Pp. 255-395.

DAHLGREN, R. M. T., H. T. CLIFFORD, and P. F. YEO. 1985. The families of the monocotyledons: structure, evolution, and taxonomy. Springer-Verlag, Berlin.

EDWARDS. A. L., D. W. LEE, and J. H. RICHARDS. 2003. Responses to a fluctuating environment: effects of water depth on growth and biomass allocation in *Eleocharis cellulosa* Torr. (Cyperaceae). Can. J. Bot. 81:964-975.

EGOROVA, T. V. 1976. Rod 7. Bolotnica, sitnjag-*Eleocharis.* R. Br. In: A. A. Federov, ed. Flora evropejskoj chasti S.S.S.R., 2. Izd-vo "Nauka," Leningradskoe otd-nie, Leningrad. Pp. 107-118.

EGOROVA, T. V. 1980. De genere *Eleocharis* R. BR. in flora orientis extremi URSS. Novosti Sist. Vyssh. Rast. 17:65-101.

EGOROVA, T. V. and N. K. KHOI. 1980. Conspectus generum *Scirpus* L., *Eriophorum* L., *Fuirena* Rottb., et *Eleocharis* R. Br. Florae Vietnami. Novosti Sist. Vyssh. Rast. 17:54-63.

EGOROVA, T. V. 1981. Generis *Eleocharis* R. Br. (Cyperaceae) florae URSS systema et conspectus. Novosti Sist. Vyssh. Rast. 18:95-124.

EITEN, L. T. 1976. Inflorescence units in the Cyperaceae. Ann. Missouri Bot. Gard. 63:81-112.

ELMGREN, G. 1759. Plantarum Jamaicensium pugillus. Praeside Dn. Doct. Carolo Linnaeo publice examinandum sistit. Upsala.

FERNALD, M. L. 1918. An intergeneric hybrid in the Cyperaceae. Rhodora 20:189-191.

FERNALD, M. L. 1925. The validity of *Eleocharis quadrangulata*. Rhodora 27:37-40.

FORD, B.A., P. W. BALL, and K. RITLAND. 1991. Allozyme diversity and genetic relationships among North American members of the short-beaked taxa of *Carex* sect. *Vesicariae* (Cyperaceae). Syst. Bot. 16:116-131.

FORD, B. A., D. A. ROSS MCQUEEN, R. F. C. NACZI, and A. A. REZNICEK. 1998. Allozyme variation and genetic relationships among species in the *Carex willdenowii* complex (Cyperaceae). Amer. J. Bot. 85:546–552.

FORMAN, L. L. 1997. Notes concerning the typification of names of William Roxburgh’s species of phanerogams. Kew Bull. 52(3):523-534.

FRASER, A. and K. KINDSCHER. 2001. Tree spade transplanting of *Spartina pectinata* Link and *Eleocharis macrostachya* Britt. in a prairie wetland restoration site. Aquatic Bot. 71:297-304.

GOETGHEBEUR, P. 1986. Genera Cyperacearum. Een bijdrage tot de kenis van de morfologie, systematiek en fylogenese van de Cyperaceae genera. Doctoral thesis, Rijksunivetersiteit, Gent.

GOETGHEBEUR, P. 1987. A holosystematic approach of the family Cyperaceae. In: W. Greuter, B. Zimmer, and H.-D. Behnke, eds. Abstracts of the 14th International Botanical Congress. Botanical Museum Berlin-Dahlem, Berlin. P. 276.

GOETGHEBEUR, P. 1998. *Cyperaceae*. In: K. Kubitzki, H. Huber, P. J. Rudall, P. S. Stevens, and T. Stützel, eds. The families and genera of vascular plants Vol 4. Springer-Verlag, Berlin. Pp. 141-190.

GONZÁLEZ -ELIZONDO, M. S. 1994. *Eleocharis*. In: Davidse, G., M. S. Sousa and A. O. Chater, eds. Flora Mesoamericana, Vol. 6: Alismataceae a Cyperaceae. Universidad Nacional Autònoma de México, Ciudad Universitaria. Pp. 458-464.

GONZÁLEZ -ELIZONDO, M. S. and A. A. REZNICEK. 1996. New *Eleocharis* (Cyperaceae) from Venezuela. Novon 6(4):356-365.

GONZÁLEZ -ELIZONDO, M. S. and P. M. PETERSON. 1997. A classification of and key to the supraspecific taxa in *Eleocharis* (Cyperaceae). Taxon 46:433-449.

GONZÁLES-ELIZONDO, M. S., P. M. PETERSON, and I. GRANZOW-DE LA CERDA. 1997. A cladistic and phenetic analysis of the *Pauciflorae* group of *Eleocharis* (Cyperaceae). BioLlania 6:341-368.

GONZÁLEZ -ELIZONDO, M. S. and J. A. TENA-FLORES. 2000. *Eleocharis* (Cyperaceae) in the New World. In: K. L. Wilson and D. A. Morrison, eds. Monocots: systematics and evolution. CSIRO Publishing. Australia. Pp. 637-643.

GONZÁLEZ-ELIZONDO, M. S. 2002. *Eleocharis* subg. *Limnochloa*. In: Flora of North America Editorial Committee, eds. Flora of North America North of Mexico, Vol. 23. Oxford Univ. Press, New York. Pp. 116-120.

GONZÁLEZ-ELIZONDO, M. S., M. GONZÁLEZ-ELIZONDO and S. G. SMITH. 2002. *Eleocharis obtusetrigona* (Cyperaceae) new to North and Central America. Acta Bot. Mex. 60:7-11.

GORDON-GRAY, K. D. 1995. Cyperaceae in Natal. Strelitzia 2. National Botanical Institute, Pretoria, South Africa.

GRANT, V. 1971. Plant speciation. Columbia University Press, New York.

GRAY, S. F. 1821. A natural arrangement of British plants, Vol. 2. Baldwin, Cradock, and Joy, London.

GREGOR, T. 2003. *Eleocharis mamillata* - distribution and infraspecific differentiation. Folia Geobot. 38:49-64.

GREUTER, W., J. MCNEILL, F. R. BARRIE, H. -M. BURDET, V. DEMOULIN, T. S. FILGUEIRAS, D. H. NICOLSON, P. C. SILVA, J. E. SKOG, P. TREHANE, N. J.

TURLAND, and D. L. HAWKSWORTH. 2000. International Code of Botanical Nomenclature (Saint Louis Code). Regnum Veg. 138:1-474.

HAINES, R. W. and K. A. LYE. 1983. The sedges and rushes of East Africa. East African Natural History Society, Nairobi.

HENDERSON, A. and E. FERREIRA. 2002. A morphometric study of *Synechanthus* (Palmae). Syst. Bot. 27:693-702.

HENRY, A. N. and M. CHANDRABOSE. 1980. An aid to the International Code of Botanical Nomenclature. Today and Tomorrows Printers and Publishers, Delhi.

HESS, H. 1953. Über die Gattungen *Heleocharis* und *Carex* aus Angola und dem unteren Kongo. Ber. Schweiz. Bot. Ges. 63:317-359.

HESS, H. 1957. Beiträge zur Kenntnis der Gattung *Heleocharis* in Brasilien. Ber. Schweiz. Bot. Ges. 67:91-94.

HINES, D. M. 1975. A monograph of the *Eleocharis ovata* complex (Cyperaceae) in North America. Ph.D. Dissertation. University of Michigan, Ann Arbor.

HOLM, L. G. 1977. The World's worst weeds: distribution and biology. University Press of Hawaii, Honolulu.

HOLMGREN, P. K., N. H. HOLMGREN, and L. C. BARNETT. 1990. Index herbariorum Part I: The herbaria of the world. New York Botanical Garden. New York.

HOLTTUM, R. E. 1948. The spikelet in Cyperaceae. Bot. Rev. (Lancaster) 14:525-541.

HOOPER, S. S. 1972. *Eleocharis* (Cyperaceae). In: J. Hutchinson and J. M. Dalziel, eds. Flora of West Tropical Africa, 2nd ed. Whitefriars Press, Ltd., London. Pp. 311-314.

JOHNSON, R. A. and D. W. WICHERN. 2002. Applied multivariate statistical analysis. Prentice-Hall, Inc., Upper Saddle River, New Jersey.

JONES, S. B. and A. E. LUCHSINGER. 1986. Plant systematics. McGraw-Hill Inc., New York.

JØRGENSEN, P. M. and S. LEÓN-YÁNEZ. 1999. Catalogue of the vascular plants of Ecuador. Missouri Botanical Garden Press, St. Louis.

JUSSIEU, A. L. 1789. Genera Plantarum. Apud viduam Herissant, typographum, Paris.

KERN, J. H. 1974. Cyperaceae. In: C.G.G.J. van Steenis, ed. Flora Malesiana, Series I, Vol. 7(3), Noordhoff, Leyden. Pp. 435-753.

KLIMKO, M. 1988. Systematic studies on *Eleocharis acutangula* (Roxb.) Schult. and *Eleocharis variegata* (Poir.) Presl. Bulletin de la Societes des amis des sciences et des letters de poznan 27:69-79.

KOYAMA, T. 1961. Classification of the family Cyperaceae. Part II. A revision of the species of the Cyperaceae in Japan and its neighboring regions. Journal of the Faculty of Science, University of Tokyo, Sec. 3, Botany 8:81-148.

KOYAMA, T. 1974. Additional notes on Ceylonese Cyperaceae. Bull. Natn. Sci. Mus. Tokyo 17:65-73.

KOYAMA, T. 1985. Cyperaceae. In: M. D. Dassanayake and F. R. Fosberg, eds. Flora of Ceylon, Vol. 5. Amerind Publishing Co. Pvt. Ltd., New Delhi. Pp. 125-405.

KUKKONEN, I. 1990. On the genus *Eleocharis* (Cyperaceae) in the flora of Iranica area, with revised infrageneric classification and nomenclature. Ann. Bot. Fennici 27:109-117.

KUNTH, C. S. 1837. Enumeratio plantarum, Vol. 2. J.G. Cotta, Stuttgart.

LARSON, B. M. H. and P. M. CATLING. 1996. The separation of *Eleocharis obtusa* and *Eleocharis ovata* (Cyperaceae) in Eastern Canada. Can. J. Bot. 74:238-242.

LEPPIK, E. E. 1955. *Dichromena ciliata*, a noteworthy entomophilous plant among Cyperaceae. Amer. J. Bot. 42:455-458.

LESTIBOUDOIS, T. 1819. Essai sur la familles des Cyperacees. Impr. de Didot Jeune, Paris.

LESTIBOUDOIS, T. 1827. Botanographie Belgique, Vol. 2. Roret, Paris.

LINNAEUS, C. 1759. Systema Naturae, Tomus II, editio decima, reformata. Laurentii Salvii, Stockholm.

LOVELESS, C. M. 1959. A study of the vegetation in the Florida Everglades. Ecology 40:1-9.

MENAPACE, F. J. 1991a. A revision of the genus *Eleocharis* (Cyperaceae) section *Maculosae*. Ph.D. Dissertation. Southern Illinois University, Carbondale.

MENAPACE, F. J. 1991b. A preliminary micromorphological analysis of *Eleocharis* (Cyperaceae) achenes for systematic potential. Can. J. Bot. 69:1533-1541.

MENAPACE, F. J. 1993. Achene micro-morphology as a systematic aid to the series placement of Svenson's undesignated *Eleocharis* (Cyperaceae) species. Rhodora 95:214-224.

METCALFE, C. R. 1971. Cyperaceae. Vol. 5. Anatomy of the Monocotyledons. Clarendon Press, Oxford.

MUTHUKUMAR, T, K. UDAIYAN, and P. SHANMUGHAVEL. 2004. Mycorrhiza in sedges-an overview. Mycorrhiza 14:65–77.

NACZI, R., A. A. REZNICEK, and B. FORD. 1998. Morphological differentiation in the *Carex willdenowii* complex (Cyperaceae). Amer. J. Bot. 85:434-447.

NEES VON ESENBECK, C. G. D. 1834a. No. III. Cyperaceae indicae. Praecipue juxta herbaria Wrightii, Wallichii, Roylei et Lindleyi. In: R. Wright, ed. Contributions to the botany of India. London. Pp. 69-129.

NEES VON ESENBECK, C. G. D. 1834b. Uebersicht der Cyperaceengattungen. Linnaea 9:273-306.

NEES VON ESENBECK, C. G. D. 1842. Cyperographia sive descriptio in Brasilia provenientium In: K. F. P. von Martius, ed. Flora Brasiliensis, Vol. II, Part I. Pp. 1-226.

NYBOM, H. 2004. Comparison of different nuclear DNA markers for estimating intraspecific genetic diversity in plants. Molecular Ecology 13:1143-1155.

OSOTSAPAR, Y., and B. T. MERCADO. 1976. Morphology and anatomy of [Chinese water chestnut] *Eleocharis dulcis* (Burm. f.) Trin. Kalikisan 5:332-340.

PALMA-SILVA, C., E. F. ALBERTONI, and F. A. ESTEVES. 2000. *Eleocharis mutata* (L.) Roem. et Schult. subject to drawdowns in a tropical coastal lagoon, State of Rio de Janerio, Brazil. Plant Ecology 148:157-164.

PARKER, P. G., A. A. SNOW, M. D. SCHUG, G. C. BOOTON. and P. A. FUERST. 1998. What molecules can tell us about populations: choosing and using a molecular marker. Ecology 79:361-382.

PLUNKETT, G. M., D. E. SOLTIS, P. S. SOLTIS, and R. E. BROOKS. 1995. Phylogenetic relationships between Juncaceae and Cyperaceae: insights from *rbc*L sequence data. Amer. J. Bot. 82:520-525.

POHL, R. W. 1965. Dissecting equipment and materials for the study of minute plant structures. Rhodora 67:95-96.

PROCTOR, G. R. 1984. Flora of the Cayman Islands. Her Majesty's Stationary Office, London.

RADFORD, A. E., W. C. DICKISON, J. R. MASSEY, and C. R. BELL. 1974. Vascular plant systematics. Harper and Row, New York.

RAVEN, P. H. and D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Garden 61:539-673.

RENCHER, A. C. 1998. Multivariate statistical inference and applications. John Wiley & Sons, Inc. New York.

RETTIG, J. H. 1990. Achene micromorpholgy of the *Carex nigromarginata* Complex (Section *Acrocystis*, Cyperaceae). Rhodora 92:70-79.

REZNICEK, A. A. 1990. Evolution in sedges (*Carex,* Cyperaceae). Can. J. Bot. 68:1409-1432.

RIKLI, M. 1895. Beiträge zur vergleichenden Anatomie der Cyperaceen mit besonderer Berücksichtigung der inneren Parenchymscheide. Jahrb. Wiss. Bot. 27:485-580.

ROALSON, E. H. 1999. *Eleocharis yecorensis* (Cyperaceae), a new species of spike-sedge from Mexico. Aliso 18:57-60.

ROALSON, E. H. and E. A. FRIAR. 2000. Infrageneric classification of *Eleocharis* revisited: evidence from the internal transcribed spacer (ITS) region of nuclear ribosomal DNA. Syst. Bot. 25:323-336.

ROHLF, F. J. 2000. NTSYS-pc: numerical taxonomy and multivariate analysis system, version 2.1. Exeter Software, Setauket, New York.

RÖEMER, J. J. and J. A. SCHULTES. 1817. Linnaeus' Systema Vegetabilium. Vol. 2. Stuttgart.

ROSEN, D. J. and S. D. JONES. 2004. *Eleocharis mutata* (Cyperaceae) new to the flora of North America north of México. Sida 21:1153-1160.

ROSEN, D. J. and S. L. HATCH. 2006. New records of *Eleocharis obtusetrigona* (Cyperaceae) from Central and South America. Brittonia 58 (in press).

ROXBURGH, W. 1820. Flora Indica or descriptions of Indian Plants. Serampore.

SANJAPPA, M., K. THOTHATHRI, AND A. R. DAS. 1991. Roxburgh's Flora Indica

Drawings at Calcuta. Bull. Bot. Surv. India 33:1-232.

SCHULTZE-MOTEL, W. 1967. Cyperacales. In: H. J. Conert, ed. Hegi's Illustrierte Flora von Mitteleuropa, ed. 2, Vol. II, part 1. Verlag Paul Parey, Berlin. Pp. 1-274.

SCHUYLER, A. E. 1971. Scanning electron microscopy of achene epidermis of *Scirpus* (Cyperaceae) and related genera. Proc. Acad. Nat. Sci. Phila. 123:29-52.

SCHUYLER, A. E. and W. R. FERREN. 1975. A new intertidal form of *Eleocharis olivacea* (Cyperaceae). Bartonia 43:46-48.

SCOTTI, I., A. MARIANI, V. VERONA, A. CANDOLINI, C. CENCI, and A. OLIVIERI. 2002. AFLP markers and cytotaxonomic analysis reveal hybridization in the genus *Schoenus* (Cyperaceae). Genome 45:222-228.

SIMPSON, D. A. 1987. Some problems in *Eleocharis*. Notes on Brazilian Cyperaceae III. Kew Bull. 43:127-134.

SIMPSON, D. A. and T. KOYAMA. 1998. Cyperaceae. In: T. Santisuk and K. Larsen, eds. Flora of Thailand, Vol 6, part 4. Diamond Printing Co. Thailand. Pp. 284-292.

SIMPSON, D. A. and C. A. INGLIS. 2001. *Cyperaceae* of economic, ethnobotanical and horticultural importance: a checklist. Kew Bull. 56:257-360.

SMITH, S. G. 2001. Taxonomic innovations in North American *Eleocharis* (Cyperaceae). Novon 11:241-257.

SOLTIS, D. E., P. S. SOLTIS, P. K. ENDRESS, and M. W. CHASE. 2005. Phylogeny and evolution of Angiosperms. Sinauer Associates, Inc. Publishers, Sunderland.

SPSS. 2003. SPSS for Windows release 11.2.5.1. SPSS Inc., Chicago.

STEARN, W. T. 1960. An Introduction to Robert Brown's Prodromus Florae Novae Hollandiae. In: R. Brown, Prodromus florae Novae Hollandiae et Insulae van-Diemen, facsimile edition. J. Cramer, Weinheim. Pp. v-lii.

STEARN, W. T. 1992. Botanical Latin. Fourth edition. David & Charles, England.

STEUDEL, E. G. 1855. Synopsis plantarum Cyperacearum. Stuttgart.

STEWART, A. 1911. A botanical survey of the Galápagos Islands. Proc. Calif. Acad. Sci. IV, 1:7-288.

STRANDHEDE, S. 1966. Morphologic variation and taxonomy in European *Eleocharis* Subser. *Palustres*. Opera Bot. 10:1-187.

STRONG, M. T. 2006. Taxonomy and distribution of *Rhynchospora* (Cyperaceae) in the Guianas, South America. Contr. U.S. Natl. Herb. 53:1-225.

STUESSY, TOD F. 1990. Plant taxonomy; the systematic evaluation of comparative data. Columbia University Press, New York.

SÜSSENGUTH, K. 1943. Einige neue Gattungen und der Cyperaceae aus Südamerika. Bot. Jahrb. Syst. 73:113-125.

SVENSON, H. K. 1929. Monographic studies in the genus *Eleocharis.* Rhodora 31:121–136; 167-191.

SVENSON, H. K. 1934. Monographic studies in *Eleocharis* III. Rhodora 36:377-389.

SVENSON, H. K. 1937. Monographic studies in the genus *Eleocharis.* Rhodora 39:271-272.

SVENSON, H. K. 1939. Monographic studies in the genus *Eleocharis* V. Rhodora 41:13–19; 95-104.

SVENSON, H. K. 1957. *Eleocharis* R. Br. In: N. L. Britton and L. M. Underwood, eds. North American Flora, Vol. 18. New York Botanical Garden, New York. Pp. 509-540.

TALLENT, R. C. and D. E. WUJEK. 1983. Scanning electron microscopy as an aid to taxonomy of sedges (Cyperaceae: *Carex*). Micron Microsc. Acta 14:271-272.

THWAITES, G. H. K. 1864. Enumeratio Plantarum Zeylaniae. Dulau & Co., London.

TORREY, J. 1836. Monograph of North American Cyperaceae. Ann. Lyceum Nat. Hist. New York. 3:239-448.

TREVISAN, R. and I. I. BOLDRINI. 2006. A new species of *Eleocharis* R. Brown (Cyperaceae) from Southern Brazil. Novon 16:155-157.

TUCKER, G. C. 1987. The genera of Cyperaceae in the Southeastern United States. J. Arnold Arbor. 68:361-445.

VARMA, S. K., A. K. PANDEY, and A. K. SINHA. 1989. Epidermal surface patterns of achene in *Eleocharis* R. Br. (Cyperaceae). Current Science 58:1374-1377.

VAUGHAN, J.G. and C. GEISSLER. 1997. The new Oxford book of food plants. Oxford University Press, Oxford.

WATERWAY, M. J. 1990. Systematic implications of achene micromorpholgy in *Carex* section *Hymenochlaenae* (Cyperaceae). Can. J. Bot. 68:630-639.

WILSON, K.L. 1993. *Eleocharis*. In: Harden, G.J. ed. Flora of New South Wales, Vol. 4. New South Wales University Press, Kensington. Pp. 370-376.

WUJEK, D. E., S. K. VERMA, and R. A. RUHLMAN. 1992. Achene micromorphology of some Indian Cyperaceae (*Cyperus*, *Fimbristylis*, *Pycreus*, *Scirpus*, and *Scleria*). Asian Jour. Pl. Sci. 4:1-19.

YANO, O., T. KATSUYAMA, H. TSUBOTA, and T. HOSHINO. 2004. Molecular phylogeny of Japanese *Eleocharis* (Cyperacrae) based on ITS sequence data, and chromosomal evolution. J. Plant Res. 117:409-419.

ZINSERLING, G. (Tsinzerling, Ju.D.) 1935. *Heleocharis*. In: B. K. Schischkin, ed. Flora URSS 3. Pp. 63-90.

ŻUKOWSKI, W. and M. KLIMKO. 1979. Variability of fruits in species of *Eleocharis* genus subseries *Palustres* in Poland. Bulletin de la Societes des amis des sciences et des letters de poznan 19:83-90.

APPENDIX I

REPRESENTATIVE SPECIMENS OF *ELEOCHARIS CELLULOSA* EXAMINED

NORTH AMERICA. U.S.A: Alabama: Baldwin Co.: sandy swale in pineland by Ala 180k, rd to Fort Morgan ca. 15 mi. W jct. Ala 59, 08 Jun 1971, *Kral 43099* (BRIT, GA). **Mobile Co.:** Dauphin Island, NE end of island along edge of salt marsh, 05 Jul 1974, *Taylor & Taylor 16504* (BRIT). **Arkansas: Union Co.:** salty soil at oil wells beside Union Co. 25 at a creek N of Urbana, 13 Aug 1990, *Thomas 120315* (BRIT, GA, MICH, VSC). **Florida: Bay Co.:** coastal interdunal swales on barrier island, S of US 98, just S and E of eastern end of St. Andrew Sound, at junction of Crooked Island with mainland, ca. 1.5 air miles WNW of Mexico Beach, 14 Sep 1990, *Orzell & Bridges 15305* (MICH, USF). **Brevard Co.:** Titusville, 01 Aug 1895, *Nash 2302* (GA, GH, MICH, MO, NY, PH). **Broward Co.:** Canal L 28, 21 Apr 1965, *Craighead s.n.* (USF); edge of deep canal alongside US 27 W, between SR 84 and SR 27, 14 Jun 1973, *Wooten 2241* (PH, TEX). **Collier Co.:** vicinity of Naples, ca. 1 mile N of Isle of Capri Rd., canals along US 41, 10 Oct 1962, *Cooley et al. 9090* (GH); shore of recently made lake, subdivision construction site, back beach of Gulf of Mexico, Marco Island, 07 Aug 1967, *Lakela 30961* (GH, USF). **Dade Co.:** southwest of Homestead, Everglades National Park, low tidal marshes N of Flamingo, 12 Oct 1962, *Cooley et al. 9212* (USF); Maimi, Jul 1877, *Garber s.n.* (F, GH, PH); 5 mi. S of Homestead, shallow water, 19 Aug 1953, *Sargent 6706* (GA); between Homestead and Cross Key, 21-22 Nov 1906, *Small & Carter 2435* (NY, PH [2 sheets]). **Dixie Co.:** Long Prairie, S. Fla, 01 Nov 1906, *Carter 62* (PH); US Hwy. 1, 10.6 mi N Monroe Co. line, 252326N, 802759W, fresh marsh, 21 Sep 1996, *Carter & Mears 13752* (CIIDIR, GH, K, MICH, MO, TAES, TEX, US, VSC, WIS). **Duval Co.:** marshes bordering St. Johns River, S Jacksonville, 27 Sep 1899, *Curtiss 6540* (F, GH, MO, NY [2 sheets], US). **Escambia Co.:** at Navarre on Santa Rosa Island, growing near the edge of tidal pool E of causeway, 21 May 1981, *Wilhelm & Ladd 9034* (USF). **Franklin Co.:** locally abundant in shallow water of drainage ditch, Dog Island, 23 Jul 1971, *Godfrey 70573* (LL, PH); Apalachicola, marshes, 1867, *Laurman s.n.* (PH [2 sheets]). **Gadsden Co.:** Chattahoochee, without date, *Curtiss s.n.* (NY). **Glades Co.:** NE of Lake Okeechobee and W of Kissimmee River, in water edge of standing pool of warm mineral artesian well, 02 Sep 1981, *Coile & Pierce 2454* (USF). **Gulf Co.:** tidal marsh muck flats, between Port St. Joe & Cape San Blass, 14 Jun 1960, *Godfrey & Triplett 59755* (USF). **Hernando Co.:** road to Bayport, wet sands at edge of salt marsh, 19 Jun 1958, *Kral & Kral 7025* (GA, GH, US, USF). **Lee Co.:** brackish marsh, Myers, Jul-Aug 1900, *Hitchcock 403* (F, GH, MO, NY); five miles E of Ft. Myers Beach on moist sands at edge of salt marsh, 01 Aug 1958, *Kral & Kral 7538* (USF); S side of Griffin Rd., just S of entrance to Pinewood Lakes in Gateway, ca. 0.5 mi E of jct Gateway Blvd, ca. 9 mi SE of downtown Fort Myers, 14 Sep 1990, *Orzell & Bridges 22529* (BRIT, USF); Wild Turkey Strand Natural Area, about 2.5 air miles SW of the intersection of Hwy. 82 and Green Meadows Rd., SE of Fort Myers, N26^{o} 32’ 17.3” W81^{o} 42’ 12.9”, 12 Nov 2004, *Rosen & Carter 3208* (CIIDIR, MICH); Everglades, S of Long Key, 18-26 Jan 1909, *Small & Carter s.n.* (NY). **Levy Co.:** border of brackish marsh near Yankeetown, 24 Aug 1954, *Godfrey 52424* (TEX). **Liberty Co.:** very abundant in extensive stands, shallow water of borrow pit, by Fla Rt. 379, about 3/4 mi. from its junction with Rt. 65, NW of Sumatra, 15 Sep 1979, *Godfrey 77249* (GA). **Monroe Co.:** Key West, without date, *Blodgett s.n.* (NY); small pond, thicket on Sugarloaf Key, in limestone, 25 Sep 1973, *Correll & Correll 40130* (MO); Duck Key, 1885, *Curtiss s.n.* (NY); Big Pine Key, along east-west street running along N side of prison, 0.5 mi. N of US 1, 18 Aug 1987, *Hansen & Richardson 11433* (USF); moist soil of nearly dry sinkhole, about .5 m W of artificial lake, Big Pine Key, 23 Mar 1951, *Killip 41058* (GA); depressions in shrubby coastal rock barren on E side of Tampa Rd., 0.4 mi S of Miami Ave., 11 Aug 1992, *Orzell & Bridges 20409* (USF [2 sheets]); lower Sugar Loaf Key, wet saline flats, 22 Aug 1953, *Sargent 6698* (SMU); Boca Chica Key, 27 Nov 1912, *Small 3944* (GH, NY, US). **Palm Beach Co.:** Corbitt Wildlife Management Area, NW of Loxahatchee, 05 Sep 1957, *Kral*

5751 (SMU). **Pinellas Co.:** slough near Lake Maggiore, 21-28 Dec 1949, *Thorne 9512* (GH). **Santa Rosa Co.:** shore of Pensacola Bay, 19 Sep 1884, *Curtiss 3080* (US); Santa Rosa Id., 30 May 1903, *Tracy 8661* (F, GH, MO, NY, PH, WIS). **Seminole Co.:** 2 mi. E of Geneva, 29 Jun 1957, *Kral 5102* (GH, SMU). **Taylor Co.:** near Adams Beach, 16 Aug 1957, *Godfrey 55900* (GH, SMU). **Volusia Co.:** floodplain pothole, upper St. John's River, 15 Sep 1971, *Auth 104* (USF [2 sheets]). **Wakulla Co.:** common on muck of pond near lower Ochlockenne River 5 mi. SE of Sopchoppy, 01 Aug 1956, *Kral 3030* (GA, GH, NY, USF [2 sheets]); very common rhizomatus clump-former in 6 in. water of pond 2 mi. S of Panacea, 01 Aug 1956, *Kral 3026* (GH, NY, GA, SMU); very abundant in standing water of a ditch along road 59, about 6 mi. N of St. Marks lighthouse, 20 Jun 1956, *Redfearn & Kral 2477* (GA, GH, NY, TEX). **Georgia: Camden Co.:** artesian overflow along highway, 3 mi. S of the Glynn Co. line on US 17, 05 October 1940, *Eyles 7628* (GH [2 sheets]); Kings Bay Submarine Base, Etowah Park, W bank of Etowah Pond, 304900N, 813245W, 28 Aug 1996, *Carter 13598* (CIIDIR, GH, K, MICH, MO, TAES, TEX, US, VSC, WIS). **Clinch Co.:** edge of small pond along Rt. 37, about 6 miles W of Homerville, 29 Jun 1998, *McNeilus 98-451* (MICH, TEX). **Louisiana: Calcasieu Parish:** ca. 5 miles S of Jct. of Hwys. LA 385 and LA 3092, along Hwy. LA 385 S to A. LeBleu Rd., then W ca. 2 miles to point where LeBleu Rd. turns S, S of Black Bayou and E of Intracoastal Waterway, 09 Sep 1992, *Carter et al. 10552* (MICH, NY, VSC). **Cameron Parish:** pond at the end of the Pines Ridge, near Sabine Lake, 31 Oct 1963, *Valentine s.n.* (SMU). **Ibberville Parish:** without location, 1883, *Langlois 149* (GH). **Iberia Parish:** in wet sand at edge of upland lake, Avery Island, 27 Sep 1963, *Thieret 16381* (WIS, SMU). **Lafayette Parish:** Lafayette, near National Wetland Research Center, 700 Cajundome Blvd., 18 Aug 1998, *Bryson 16622* (VSC). **Plaquemines Parish:** Pointe a la Hache, in rice fields, Jun 1882, *Langlois s.n.* (NY, PH). **St. Tammany Parish:** Big Branch Marsh National Wildlife Refuge, marsh edge S of Boy Scout Road boardwalk, 25 Sep 1999, *Rosen 896* (NO). **Mississippi: Hancock Co.:** 8 mi. NW of Bay St. Louis, 11 Jul 1964, *Sargent 8294* (SMU). **Harrison Co.:** Biloxi, 22 Jun 1899, *Tracy 6503* (GH, MO, NY). **Jackson Co.:** Horn Island, 27 Jun 1901, *Tracy 7680* (F, GH, MO, NY, WIS); Ocean Springs, 02 Sep 1889, *Tracy s.n.* (NY). **North Carolina: Dare Co.:** 3 mi W of Old Cape Hatteras Lighthouse, Hatteras Island, E of Pamlico Sound, 15 Oct 1940, *Fosberg 17965* (MICH). **South Carolina: Georgetown Co.:** NE side of Cat Island Plantation, Cat Island, 04 Sep 1992, *Nelson & Kennemore 13,440* (MICH). **Texas: Aransas Co.:** shallow water pond 36° and 20 km from the town of Fulton, 16 Sep 1990, *Churchill 90-909* (WIS). **Bexar Co.:** San Antonio, 08 Jul 1911, *Clemens & Clemens 395* (PH). **Brazoria Co.:** In wet, open roadside ditch, S of CO RD 2004, about 11.5 miles E of Hwy. 288, between Hitchcock and Lake Jackson, 10 Jun 2004, *Rosen 2968* (BRIT, CIIDIR, VSC, SBSC). **Calhoun Co.:** South of Hwy. 185, 4.1 miles E of Seadrift, 24 Jul 2004, *Rosen & Combs 3018* (CIIDIR, GH, K, MICH, MO, TAES, TEX, US, VSC, WIS). **Cameron Co.:** large wetland depression W of “County” Rd., about .5 air miles NW of where it crosses Resaca de los Cuates, near the NE corner of Laguna Atascosa, 29 Oct 2004, *Rosen & Jones 3180* (TAES, VSC). **Chambers Co.:** N side of Sykes Rd., 0.8 mi W of Oyster Bayou Bridge, 10 Sep 1992, *Carr & Carter 12316* (TEX). **Comal Co.:** Comal Springs, mouth of spring run no. 2, 15 Jul 1996, *Rosen 194* (SWT). **Galveston Co.:** costal prairie S of Hitchcock, about 2.7 miles S of the intersection of Hwy. 6 and FM RD 2004, 19 Aug 2004, *Rosen 3051* (BRIT, TEX). **Gillespie Co.:** swampy margins of creeks about Fredricksburg, Sep 1847, *Lindheimer 719* (GH [2 sheets], MO). **Gonzales Co.:** without location, 05 Mar 1928, *Tharp s.n.* (GH, TEX). **Guadalupe Co.:** ca. 2 mi. E of junction Alt. US Rt. 90 and St. Rt. 123 bypass on E side of Seguin, 04 Sep 1993, *Carr & Turner 12973* (TEX). **Harris Co.:** LaPorte, along Underwood Street at intersection with North Street, 06 Aug 1983, *Brown 6452* (BRIT). **Jefferson Co.:** J. D. Murphree Wildlife Management Area, 1-10 mi. SW of Port Arthur, 20 Oct 1966, *Stutzenbaker 124* (TEX). **Kennedy Co.:** 2.7 miles S of Armstrong, wetland along W sode of Hwy. 77, 18 Sep 04, *Carter 15755* (CIIDIR, GH, K, MICH, MO, TAES, TEX, US, VSC, WIS); E of US HWY. 77, about 4.6 miles N of Armstrong, N26° 59’ 28.6” W97° 47’ 41.3”, 30 Oct 2004, *Rosen & Jones 3198* (TAES, VSC). **Kerr Co.:** Ingram, Aug 1935, *Kenoyer 211* (TEX). **Kleberg Co.:** Padre Island National Seahore, Malakite Beach, ca. 19 miles SW of the intersection of ark Road 22 and

FM 361, S of the city of Corpus Christi, 06 Nov 2004, *Wallgren s.n.* (TAES). **Mason Co.:** along the Llano River, 7 miles SW of Mason, 04 Jul 1963, *Correll et al. 28253-B* (TEX). **Nueces Co.:** E side of N-S runway, ca. 200-00 ft. N of Yorktown Blvd., ca. 0.3 mi. W of Waldron Rd., Naval Auxiliary Landing Field Waldron, 11 Sep 1992, *Carr & Carter 12347* (TEX). **Orange Co.:** Gun Tree Island Rd. of the lower Nueches Wildlife Management Area, 17 Oct 1998, *Stewart 15* (TAES). **Real Co.:** Frio River above Leakey, 26 Jul 1951, *Tharp et al. 51-1635* (PH, SMU, TEX). Garner State Park, 12 Jul 1952, *Webster 4314* (MICH, SMU, TEX). **Val Verde Co.:** shallow water pond 36^{o} and 20 km from the town of Fulton, 16 Sep 1990, *Churchill 90-909* (WIS); Devils River, 12.5 mi NW of Del Rio , 16 Aug 1941, *Cory 38020* (TAES). **MEXICO: Estado de Campeche:** Canal de la Laguna El Vapor, El Carmen, Lat 18^{o} 25, Lon 91^{o} 50, 26 Oct 1989, *Ocana-Nava & Coronado 342* (MEXU); Municipio Calkini**,** Camino El Remate-Isla Arena, Manglar en la Orilla Del Camino., 20-32 N, 90-20 W, Nivel Del Mar , 08 Nov 1980, *Rico-Gray 220* (F). **Estado de Nuevo Leon:** on floating island in Ojo de Aqua a 1 Nogolar, 18 Aug 1944, *Barkley 14587* (F, GH, MO, NY); Linares, Banos de San Ignacio, 16 Jun 1987, *Gonzalez 4013* (CIIDIR, MEXU). **Estado de Quintana Roo:** Chachankanab, without date, *Gaumer 1447* (F); Coba, Lake Coba, Jun-Jul 1938, *Lundell & Lundell 7796* (US); Pequena islet, a y bordes de la Laguna de Bacalar, 24 Oct 1976, *Novelo 306* (MEXU, MO); Lake Chichancanab (Laguna Chan-kabnab), 28-29 Jul 1932, *Swallen 2733* (F, MICH, US). **Estado de Tabasco :** La Palma, Balancan, river side, 01-06 Jun 1939, *Matuda 3259* (F, GH) ; Selva inundable cercana al camino que va a la Pera y pozo petrolero el Espadanal, cerca de la desviacion a el Faisan, aproximadamente 10 km al sur de Nueva Centla, Mpio. Centla 5 m, Lat 18^{o}32'6.3" Lon 92^{o}33'21.3", 10 Sep 1998, *Novelo & Ramos 2781* (MEXU). **Estado de Tamaulipas :** river at Altamira, 03 Jun 1939, *LeSuer 36* (TEX). **Estado de Veracruz-Llave:** Borde norte de Laguna Salada Transecto Punta Limon, 27 Jun 1972, *Lot 2090* (F, MO). **Estado de Yucatan:** Municipio Telchac Puerto, ca. 20 km N of Dzemul, near the coast, elev. 2 m, marsh at edge of mangrove, 28 Oct 1984, *Davidse & Davidse 29471* (MEXU, MO); Municipio Progreso, ca. 4 km S of El Pogreso on Hwy. 273 to Merida, elev 5 m, 20 Oct 1984, *Davidse & Davidse 29447* (MO); 8 km antes de Sisal, 5 msm M, Bosque espinosa inundable, 28 Oct 1984, *Espejo 1314* (MO) ; Progreso, without date, *Gaumer 2402* (F, GH, K, P); Progreso, in brackish marsh S of cienaga, 30 Jul 1938, *Lundell & Lundell 8211* (LL, MICH, US); Laguna de Chichancana, a 5 km de la Carretera Peto-Polyuc, 27 Oct 1976, *Novelo 337* (GH); Mun. San Felipe, 100 m, al S de playa Chisascab, reserva de Dzilam, 213145N, 883125W, 20 May 1992, *Trejo 198* (MEXU). **CENTRAL AMERICA. GUATEMALA: Departamento de Guatemala:** Amatitlan, Lake Amatitlan, 05 Feb 1905, *Kellerman 4781* (US). **Departamento del Peten:** Peten, lakeshore, N shore Lake Peten near junct. Rd. to Tikal and rd to Flores, 13 Jul 1972, *Dwyer & Pippin 10229* (F); Lake Peten, 14 Jun 1933, *Lundell 3974* (MICH). **BELIZE: Belize District:** 09 Aug 1992, *Worthington 21209* (MO, NY). **HONDURAS:** Honey Camp, coastal region, Oct 1929, *Lundell 575* (F, GH, MO, NY); pool in pine ridge near Manatee Lagoon, 21 Jun 1905, *Peck 57* (GH). **NICARAGUA: Departamento de Chontales:** vicinity of Juigalpa, 4-13 Jun 1947, *Standley 9337* (F). **Departamento de Granada:** Hacienda El Hatillo, pantanos y potreros inundados, 12^{o}01'N, 85^{o}55'W, 10 Sep 1982, *Sandino 3552* (MO). **CAICOS ISLANDS:** Pine Cay, 25 Aug 1974, *Correll 43135* (F, GH, MO, NY, TEX).

CARIBEAN BASIN. BERMUDA: Waterwick marsh, 31 Aug-20 Sep 1905, *Brown & Britton 305* (F, GH, NY, PH). **BAHAMA ARCHIPELAGO: Abaco:** opposite Cherokee settlement, 05 Jan 1904, *Brace 2066* (F, NY). **Acklins Island:** in water of open pond near Pinefield, 07 June 1976, *Correll et al. 47254* (MO, NY). **Andros:** earing Point, 18 Aug-10 Sep 1906, *Brace 5312* (F, NY). **Cat Island:** by roadside 0.5 mi. N of Arthurstown, 01 Aug 1968, *Byrne 576* (GH, NY, WIS); Dumfries, 21 Nov 1975, *Correll 46174* (F, NY). **Crooked Island:** 09-23 Jan 1906, *Brace 4800* (F, NY). **Eleuthera:** about 3 miles N of Tarpum Bay, 14 Aug 1977, *Correll & Correll 48973* (MO, NY, SMU). **Grand Bahama:** Pelican Lake area, 08 Nov 1973, *Correll 40664* (MO). **Great Abaco:** along roadway between Marsh Harbour and airport, near U.S. Missile tracking station, 05 Jul 1974, *Correll & Popenoe 42591* (NY, TEX). **Great Bahama:** 16 Apr-08 May 1905, *Brace 3559* (F, NY). **Great Exuma:** 22-28 Feb 1905, *Britton & Millspaugh*

2928 (F, NY). **Great Inagua:** in water of quarry pits on Maroon Hill, 25 Jul 1976, *Correll 47521* (MO, NY, SMU). **Long Cay:** 07-17 Dec 1905, *Brace 4117* (F, NY, US). **Long Island:** just S of Grays, 19 Nov 1977, *Correll 49146* (F, MO, NY). **New Providence:** swamp, Clifton, 13 Sep 1904, *Brace 755* (F, NY); freshwater swamp, Siniturest (sic) Bay, 03 Sep 1904, *Britton & Brace 505* (F, GH, MO, NY, PH). off Coral Harbour Road near airport, 07 June 1979, *Correll 50733* (F, MO, NY). Southwest Bay area, 5-Oct-77, *Correll 49047* (MO, NY); in large stands in shallow water of ponds at Camp Site W of Adelaide, along SW Road, 19 Apr 1977, *Correll 48449* (NY); in water of feshwater ponds on Coral Harbour Golf Course, 19 Sep 1978, *Correll 50208* (MO); in water of south border of Lake Cunningham, 02 Nov 1973, *Correll & Popenoe 40414* (NY); marsh along Independence Drive, just W of Prince Charles Ave., Nassau, 26 Jun 1979, *Correll & Popenoe 50754* (NY); marsh along Independence Drive, just W of Prince Charles Ave., Nassau, 26 Jun 1979, *Correll & Popenoe 50754* (MO); Hog Island, 03 Jun 1909, *Wilson 8362* (F, NY). **San Salvador Island:** E of Granny Lake, E side of island, 14 Jun 1978, *Smith et al. 4899* (SMU). **South Andros:** in water of small borrow pit, Kemp's Bay, 23 Sep 1974, *Correll 43451* (GH [2 sheets], NY, SMU, TEX). **South Bimini:** fresh water pond, May 1948, *Howard & Howard 10235* (GH [2 sheets], NY, SMU). **CUBA: Provincia de Camaguey:** Ganado, Cayo Sabinal, 17-18 Mar 1909, *Shafer 885* (NY). **Provincia de La Habana:** Balabarro (Batabano?), 02 Oct 1904, *del Pino 2273* (NY). Isle of Pines**,** Coe's camp, Ensenada de Siguanea, mangrove swamp, 25 Feb 1916, *Britton & Wilson 14837* (NY); along Rio Las Casas, below Nueva Gerona, 03 Feb 1953, *Killip 42563* (GH, US); Pinar del Rio, Jovero to Las Martinas, across the Cienaga on a rodway under several feet of water, 18 Dec 1911, *Shafer 11055* (GH, NY). **JAMAICA: Parish of St. Elizabeth:** Salt Spring to Broad River, 28 Dec 1962, *Adams 12,057* (MO). **Parish of Manchester:** near Gut River, 25 Jul 1979, *Fairbairn et al. s.n.* (MICH). Along the banks of Black River, 02 Sep 1917, *Harris 12,558* (K). **HAITI: Departement de l' Artibonite: v**icinity of Etang, Etang Sumatre, 04-12 Apr 1920, *Leonard 3484* (NY). **DOMINICAN REPUBLIC: Provincia de Independencia :** Hoya de Enriquillo, en la orilla del Lago Enriquilla, directamente al sur de Postrer Rio, 27 May 1987, *Zanoni et al. 39399* (GH, NY). **PUERTO RICO:** Condado, 19 Mar 1922, *Britton et al. 6636* (NY); Arecibo, Vega Baja, 09 Nov 1960, *Gonzalez 1080* (NY); San Juan, 05 Nov 1913, *Hess 4070* (NY).

SOUTH AMERICA. VENEZUELA: Estado Guarico: Infante, Parque Nacional Aguaro-Guariquito, congriales de la Gorra, entre La Esperanza y Mesa de Cambao, ca. 9°12'-9°16' lat N, 67°48'-67°60' long W, Dec 1981, *Delascio et al. 11222* (MO).

APPENDIX II

ELEOCHARIS MUTATA SPECIMENS EXAMINED

NORTH AMERICA. U.S.A: Texas: Brazoria Co.: Hoskin’s Mound, 3.8 km SE of intersection of FM 2004 and Co. Rd 277, 21 Oct 2002, *Rosen & Jones 2382* (MO, TAES, TEX, VSC), 29 Aug 2003, *Rosen 2606* (GH, SBSC, NY, US, WIS, Z), *Rosen 2614* (CIIDIR, K, MICH). **Goliad Co.:** 16 mi. W of Goliad, 23 Aug 1941, *Glazener s.n.* (TAES, US). **MEXICO: Estado de Campeche:** a 15 km al sur de Sabancuy, 27 Mar 1982, *Cabrera 2278* (MEXU, MO); Xiquichak, al E de Seybaplaya, 24 Nov 1977, *Lot 2557* (GH, MEXU); Carretera sabuncuy-Escarcega 1 km, 04 Sep 1976, *Menendez 486* (MO); Sobre el Rio Mamantel (Ribera), Fente al Pital, 06 Sep 1976, *Menendez 526* (MO); Carr. Champoton isla Aguada, km 90 direccion W Champoton, 19^{o} 05, 91^{o}10, Tular-Carrizal Primario Suelo, 27 Sep 1984, *Ortiz 673* (MEXU). **Estado de Chiapas:** Tonala, mangrove swamp and silted margins of small stream on the E shore of Mar Muerto, N of Peredon, 18 Oct 1971, *Breedlove & Thorne 20805* (MO). **Estado de Coahuila de Zaragoza:** Rio Monclova, elev. 200 ft., 5-7 Jul 1939, *White 1770* (GH, MICH). **Estado de Colima:** Revillagigedo Islands, Clarion Island, Sulphur Bay, 27 Mar 1932, *Howell 8357* (GH, NY, US). **Estado de Guerrero:** Coyuca de Benitez, El Tular, frente a Los Mogotes, 16^{o} 56' 53", 100^{o} 04' 45", 12 ene (sic) 1987, *Soriano 126* (MEXU). **Estado de Jalisco:** about 2 km N of Puerto Vallarta, 13 Nov 1963, *Feddema 2533* (MICH); La Huerta, Rancho Cuixmala, Gargollo farm, on E side of Cerro de la Alborada, 19^{o} 24', 104^{o} 59', 04 Nov 1991, *Lott et al. 4116* (K, MEXU, MICH, MO, NY, WIS); Rancho El Paraiso, a ca 4 km al SE de la Estacion Carr. a Barra de Navidad, 01 Nov 1982, *Lott et al. 1555* (MEXU [2 sheets]); Cuixmala, entre la Manzanillera y la vena del rio, Mpio. La Huerta, 28 Apr 1987, *Perez 2047* (MEXU); 3 km al N de Puerto Vallarta, 16 Nov 1963, *Rzedowski 17829* (MICH). **Estado de Quintana Roo:** Bajo inundable del Rio Hondo a la altura de Alvaro Obregon a 54 km, de Bacalar rumbo a al Union, 17 Jul 1979, *Lot & Novelo 784* (GH). **Estado de Tabasco:** Laguna Redonda, 35 km W of Paraiso, 01 May 1963, *Barlow 21/1* (GH, WIS); Mecoacan, 16 May 1963, *Barlow 28/14* (US, WIS); Mecoacan, 16 May 1963, *Barlow 28/14 C* (US); SE and E Laguna Mecoacan, 16 May 1963, *Barlow 28/14B* (MEXU); a 2 km del pueblo Tabasquillo, 21 Jun 1999, *Guadarrama et al. 6749* (MEXU); alrededores de Paso San Roman, 08 Dec 1983, *Gutierrez 1381* (MEXU; WIS); Borde del rio Tonala, en el ejido el Paraiso, en donde hay varias instalaciones de PEMEX, Huimanguillo, 30 Jan 1999, *Novelo & Ordonez 2009* (MEXU); Rio Tonala, entre Agua Dulce y las Choapas, Borde de los estados de Tobasco y Veracruz, Huimanguillo, 30 Jan 1999, *Novelo & Ordonez 1871* (MEXU [2 sheets]); Reserva de la Biosfera Pantanos de Centla, Laguna San Pedrito, Centla, 8 m, 18^{o} 26'8", 92^{o} 38'6", 04 Dec 2002, *Novelo & Ordonez 4535* (MEXU [2 sheets]); Comalcalco, 14 Jun 1996, *Ortiz 2024* (MEXU); Cardenas, en el campo petrolero San Ramon en el Ejido San Ramon, 17 Jun 1996, *Ortiz 2065* (MEXU); Cabezal 31 de Pemex, Colonia Caparroso, Centla, 13 Jun 1997, *Ortiz et al. 5067* (MEXU); Mpio. Cárdenas, Ejido Miguel Hidalgo, 7.9 km E of the town of La Venta, along the road to Benito Juarez, 12 Jul 2006, *Rosen et al. 3861* (CIIDIR, GH, K, MICH, MO, TAES, TEX, US, VSC, WIS). **Estado de Tamaulipas:** Laguna del Chairel Sur. Tampico, 12 Jul 1985, *Olivo 85* (MEXU). **Estado de Veracruz-Llave:** 2 km de Las Choapas Atras del Rancho El Roble, 18 Sep 1974, *Adlosx? 52* (GH); 14 mi. SE of Tantoynca on Mexico Federa; Rte 105, 22 Sep 1971, *Keil & Canne 9226* (PH); Laguna de Sontecomapan, Isla Coscoapan, Catemaco, 11 Feb 1973, *Menendez 47799* (MO); Mpio. Agua Dulce, rancho La Azucena, S roadside of westbound lanes of Hwy. 180D, E of the city of Coatzacoalcos, ca 3.6 km W of the Rio Tonala, 13 Jul 2006, *Rosen et al. 3869* (MICH, TAES, TEX, US, VSC). **Estado de Yucatan:** a 8 km al SE de Sisal, 11 Aug 1978, *Lot 2582* (MO).

CENTRAL AMERICA. GUATEMALA: Departamento de Huehuetenango: Cienaga de Lagartero, below Miramar, alt. 300 m, 29 Aug 1942, *Steyermark 51541* (NY). **BELIZE: Belize District:** roadside through mangrove swamp, 11 Mar 1933, *Lundell 1816* (MICH); Belize City, swamp on S side of town, 09 Aug 1992, *Worthington 21439* (MO); mile 15, western highway, 26 Jul 1971, *Vaughan 276B* (MO). **Toledo District:** Monkey River, 18 Oct 1941, *Gentle 3708* (GH, MICH, MO, NY, US). **CLIPPERTON ISLAND:** SW side of island, 11 Aug 1958, *Sachet 317* (NY, P, US). **HONDURAS: Departamento de Atlantida:** Tela beach, 11 Apr 1970 , *Molina & Molina 25732* (MO); vicinity of Ceiba., 06 Jul 1938, *Yuncker et al. 8243* (GH, MICH, MO, NY). **Departamento de Francisco Morazan:** Monte Redondo lake, vicinity of Yeguare river, El Eamorano, 23 Jan 1970, *Molina 25403* (GH, LL, MO, NY); vicinity of Agua Amarilla and Hoya Grande, 27 Oct 1989, *Molina 34171* (MO). **Departamento de Valle:** 3 km E of San Lorenzo along the road to the new sea harbor, 05 Oct 1986, *Davidse & Pilz 31679* (MO). Sibun River, 28 Nov 1934, *Gentle 1429* (MICH, MO, NY). Hector Creek, Sibun River, 28 Nov 1934, *Gentle 1432* (K, MICH, MO, NY, US). Ca. 1 mile W of Belize, 1977, *Huston 514* (MO). All pines, 23 Jan 1970, *Schipp 786* (GH, MICH, MO, NY, Z). Northern Hwy. 4 miles NW from Belize, 09 Aug 1970, *Wiley 188* (MO, WIS). **NICARAGUA: Departamento de Leon:** km 65 Carretera Vieja a Leon, 12° 18'N, 86° 41'W, elev. 60-70 m, 01 Jul 1982, *Sandino 3192* (CIIDIR, MO). **Departamento de Managua:** the mouth of Rio El Carmen, 30 km NW of Masachapa, 16 Nov 1976, *Neill 1276* (MO); near the mouth of Rio El Carmen, 30 km NW of Masachapa, 16 Nov 1976, *Neill 1279* (CIIDIR). **Departamento de Zelaya:** El Bluff, near Bluefields, 14 Dec 1968, *Dudey 609* (MO, NY); area de la Bahia de Bluefields, Rio Escondido, en pantano, Rio Escondido, pantanos de Schooner Cay, 31 Mar 1949, *Molina 2041* (US); en pantano, Rio Escondido, pantanos de Schooner Cay, area de la Bahia de Bluefields, 31 Mar 1949, *Molina 2041* (GH, MO); Monkey Point, 1.5 km al NW, 11° 36'N, 83° 38'W, 21 Oct 1981, *Moreno & Sandino 11984* (CIIDIR, MO); El Bluff near Bluefields, 14 Dec 1968, *Seymour 642* (BRIT, GH, MO); Rama Cay, Bahia de Bluefields, ca 11° 52'N, 83° 48'W, 09 Apr 1981, *Stevens 20042* (CIIDIR, MO); Corn Island, 06 Mar 1971, *Svenson 4317* (BRIT, CIIDIR, GH); Puerto Cabezas, 13 Mar 1971, *Svenson 4653* (MO, SMU). 0.3 km N of intersect with rd to Tipitapa by Pan Amer. Hwy., 26 Jun 1982, *Kral 69086* (MO). Comarca del Cabo, margins of pond, 16 Mar 1971, *Svenson 4871* (NY, SMU). **COSTA RICA: Provincia de Guanacaste:** Laguna Palo Verde, Parcela, Parque Nacional Palo Verde, 24 Aug 1992, *Chavarria 669* (MO); 1 km E of Rio Tempisque ferry, 21 Oct 1984, *Crow 6112* (MO); Refugio de Fauna Silvestre, 10° 20' 30"N, 85° 20' 30"W, 21 Oct 1989, *Crow 7437* (MO, WIS); Palo Verde National Park, 07 Sep 1984, *Crow & Rivera 5981* (MO); Palo Verde National Park, 01 Aug 1987, *Crow et al. 6909* (MO, WIS). **Provincia de Limon:** N shore of the mouth of the Rio Colorado at Barra de Colorado, between the village and the Caribbean Sea, 83° 35' 30"W, 10° 47' 40"N, 12 Sep 1986, *Davidse & Herrera 30952* (MO); marsh behind storm beach of the Caribbean Sea between Limon and Rio Banano, 16 Sep 1968, *Davidse & Pohl 1235* (MO); Limon airport, beach at mouth of Rio Banano; near sand dunes and shallow ponds 35 m from shore., 07 Jul 1966, *Denton 1139a* (MICH). Limen, Nov 1896, *Pittier & Tonduz 10342* (M). **PANAMA: Provincia de Bocas del Toro:** along road W Almirante, 17 Oct 1965, *Blum 1415* (MO). **Provincia de Panama (Canal Zone):** Farfan Beach road, 03 Aug 1967, *Kirkbride & Elias 69* (MO, NY); between Corozal and Ancon, Sep 1914, *Pittier 6775* (GH, NY, US); near Fort Randolph, 28 Dec 1923, *Standley 28632* (US). **Provincia de Colon:** 04 Jun 1874, *Kuntze 1819* (NY). **Comarca de San Blas:** Rio Urgandi (Rio Sidra), 27 Jun 1986, *de Nevers & Herrera 8105* (MO).

CARIBEAN BASIN. BAHAMA ARCHIPELAGO: Eleuthera Island: NE edge of North Palmetto, 16 Aug 1977, *Correll & Correll 49001* (MO, NY). **CUBA: Provincia de Ciudad de La Habana:** boros de la riviere du Cano, Nov 1910, *Leon 1704* (P); vicinity of Guanabacoa, 02 Apr 1910, *Britton et al. 6248* (NY); Near Marianao, Nov 1908, *Leon 751* (NY); Rio del Cans, El Cano, 28 Jul 1910, *Leon, 1704* (NY); N of Columbia Camp, near Havana, 12 Dec 1912, *Leon 3668* (NY); Fiuca Europa-Guauimar, 17 Jun 1915, *Leon 5071* (NY); near Playa de Mariauao, Oct 1915, *Leon & Hioraw 5699* (NY); Province of Havana, 10 Apr 1903, *Shafer 156* (NY). **Provincia de Matanzas:** Caveleuas, 31 Aug 1903, *Britton & Wilson 174* (NY); 1860-1864, *Wright 3375* (GH [mixed with *E. acutangula*], P). **CAYMAN ISLANDS: Grand Cayman Island:** Red Bay, 23 June 1938, *Kings 102* (NY). **JAMAICA: Parish of St. Andrew:** near Kingston, 16 Mar 1936, *Hunnuerll & Griscom 14125* (GH). Bluefields and vicinity, 22 Sep 1907, *Britton 1623* (NY); vicinity of Kingston, 7-8 Mar 1910, *Brown 375* (NY). **Parish of St. Mary:** area around Green

Castle, 05 Jul 1963, *Crosby et al. 513* (GH, MICH, MO, NY, RSA, TEX). **Parish of St. Thomas:** Grant's Pen, edge of swamp, 28 Jun 1960, *Adams 7343* (M); N of Grant Pen, off of road A-4, 21 Jul 1963, *Crosby et al. 822* (GH, MICH, NY, US). Salt ponds, in marshes, 27 Oct 1915, *Harris 12310* (GH, NY); Port Antonio, Dec 1890, *Hitchcock s.n.* (MO); 1845, *Hooker* (P); Black River, 28 Nov 1976, *Proctor 36668* (NY). **HAITI: Departement du Nord-Est:** between Terrier Rouge and Fort Libertr, northeastern alluvial plain, 26 Jun 1941, *Bartlett 17480* (GH, MICH, NY, US); Oct 1906. **Departement de l' Artibonite:** vicinity of Etang, Suamatre, 4-12 Apr 1920, *Leonard 3532* (NY). **Departement de l' Ouest**: Port-au-Prince, Massif de la Pelle, Marrie-a-Bateau, 01 May 1927, *Ekman 8046* (GH, NY); 01 May 1927, *Ekman 8047* (GH [2 sheets], NY) ; Plaine Cul-de-Sac, Dept. Ouest, 18^{o} 39.5'N, 72^{o} 09' W, 27 Ene 1984, *Zanoni et al. 28765* (NY). *Buch 1083* (GH). **DOMINICAN REPUBLIC: Provincia de La Romana:** near Punta Blandino, 15 Jul 1981, *Zanoni et al. 15463* (NY). **Provincia de Peravia:** Galeon, Bani, 29 Oct 1976, *Cicero et al. 8276* (NY, TAES); Laguna Don Gregorio, NNE side of town of Don Gregorio, 18^{o} 15' N 70^{o} 12'W, 23 Sep 1980, *Mejia and Zanoni 8369* (US). **Distrito Nacional:** Santo Domingo, vicinity of Ciudad Trujillo, 07 Oct 1947, *Allard 15929* (NY, US); Santo Domingo, Valle de Cibao, prov. Santiago, Las Lagunas, Pozo Hediondo, 07 Dec 1930, *Ekman 16350* (GH, K, NY); Santo Domingo (?), La Romana, al nivel del mar, 15 Nov 1973, *Liogier 20727* (NY); City of Santo Domingo, 18^{o} 31'N 69^{o} 50'W, 17 Feb 1981, *Mejia & Ramirez 11066* (NY). **Provincia de Samana:** vicinity of Sanchez, Peninsula, 29 Nov-12 Dec 1920, *Abbott 6* (US). **Provincia Maria Trinidad Sanchez:** Llanura de Nagua, Las Gordas, 18.7 km, 19^{o} 25N, 70^{o} 00W, 05 Oct 1982, *Mejia & Pimentel 23601* (MO). **PUERTO RICO: Guayama:** Los Mareas-P.R. 710, 10 Jan 1961, *Gonzalez Mas 1307* (NY). **Isla de Culebra:** in pool, 3-12 Mar 1906, *Britton & Wheeler 172* (NY). **Isla de Vieques:** Playa Grande to La Mina, 21 Feb 1914, *Shafer 2999* (NY). **Mayaguez:** Caborojo-Joyudas-road 102, 20 Aug 1960, *Gonzalez Mas 640* (NY). Royal de Kumacau, Jun 1887, *Eggers 680* (C). Without date, *Eggers 979* (M); Caborojo-Joyudas-road 102, 20 Aug 1960, *Gonzalez Mas 635* (NY); 20 Aug 1960, *Gonzalez Mas 636* (NY); 20 Aug 1960, *Gonzalez Mas 638* (NY); Guayama, r. 707, 03 Sep 1960, *Gonzalez Mas 705* (NY); Salinas, 17 Sep 1960, *Gonzalez Mas 719* (NY); 17 Sep 1960, *Gonzalez Mas 737* (NY); Vega Baja, Tortugueas Lagon, 09 Nov 1960, *Gonzalez Mas 1056* (NY); 09 Nov 1960, *Gonzalez Mas 1063* (NY); Salinas, road 3 km 156, 10 Jan 1961, *Gonzalez Mas 1296* (NY); Arroyo, estuary, 10 Jan 1961, *Gonzalez Mas 1323* (NY); Luquillo, 65 Inf Div. Hwy Km 37.7, 12 Jan 1961, *Gonzalez Mas 1442* (NY); Arecibo, 04 Jul 1961, *Gonzalez Mas 1830* (NY); Catano, Punta Salinas, 10 Nov 1961, *Gonzalez Mas 2124* (NY); Santruce, Nov 1913, *Hioram s.n.* (NY); Rio Piedras, 22 Jun 1913, *Johnston 832* (NY); 1886, *Krug 4942* (PH); Punta Comejen, Rio Grande, 29 Aug 1979, *Liogier et al. 29224* (NY); El Vigia, Arecibo, 13 Jan 1983, *Liogier et al. 33766* (NY [2 sheets]); Yabucoa, 08 Sep 1886, *Sintenis 4942* (GH, M, NY, P, Z [2 sheets], ZT); E end of Laguna Tortuguero, 31 Dec 1980, *Solomon 5749* (MO); Martin Pena, 23 Nov 1913, *Stevenson 263* (US); Guanica lagoon, 17 Mar 1937, *Velez 1077* (NY); San Juan, 30 Feb 1960, *Woodbury s.n.* (NY); Arecibo, Tortuguero area, at sea level, 25 Mar 1982, *Alain et al. 33006* (NY); Municipio de Manati, Barrio Tierras Nuevas Saliente, area just S of Laguna Tortuguero, elev near sea level, 28 Nov 1986, *Proctor 42687* (US); Tortuguero, Feb 1963, *Woodbury s.n.* (NY). **VIRGIN ISLANDS: St. Croix island:** without date, *Eggers 31/774* (C [2 sheets]); without date, *Hansen 51* (C); St. John's, 11 Jan 1896, *Ricksecker 210* (GH, NY); Bethlehem gut, 14 Jun 1897, *Ricksecker 414* (E); Armas Hope, 28 Nov 1925, *Thompson 1043* (NY). **St. Thomas island:** Sump v/Long Bay, 19 Jan 1914, *Ostenfeld 137* (C, P). **Tortola Island:** 21 Nov 1965, *Darcy 692* (MO); 21 Nov 1965, *Darcy 693* (GH); 21 Nov 1965, *Darcy 695* (C); Purcells, 01 Jan 1919 *Fishlock 315* (NY); 01 Jan 1919, *Fishlock 316* (GH; NY). **LEEWARD ISLANDS: Anguilla Island:** back of lagoon on Road Bay, 14 Jan 1959, *Proctor 18769* (GH). **Antigua:** St. Paul, Bethesda, au SE de L'ile, 28 Dec 1981, *Raynal-Roques & Jeremie 21931* (GH, P); Weir's, 29 Dec 1936, *Box 535* (NY); road to St. Philip's, 4-16 Feb 1913, *Rose et al. 3443* (NY, US); 1849, *Wullsihlaegel* (M). **Barbuda Island:** near Bull Hole cattle pen, 29 Aug 1970, *Stoddart 3097* (US). **Montserrat:** Chance's pond, 14-18 Jun 1950, *Howard 11894* (GH, MICH); Chavers Road, 26 Jan 1907, *Shafer 298* (NY). **Nevis:** Clifton estate, 06 Mar 1959, *Proctor 19382* (GH). **WINDWARD ISLANDS: Guadeloupe.**

Basse-Terre Island: S de Petit-Bourg, 12 Jul 1984, *Jeremie 1443* (P). **Grande-Terre Island:** Vieux-Bourg, 10 Nov 1982, *Jeremie 1028* (GH, P); E Ste Anne, 16 Nov 1983, *Jeremie 1331* (GH, NY, P); NE Gosier, 13 Jul 1984, *Jeremie 1447* (P); E Ste Anne, 24 Apr 1985, *Jeremie 1535* (P); 13 Mar 1963, *Stehle 8061* (P); Gosier, Grande Ravine, 13 Jul 1984, *Jeremie 1446* (P). **La Desirade Island:** Baie-Mahault, 13 Jun 1960, *Proctor 21325* (GH). **Marie-Galante Island:** marais de Folle Anse, 18 Nov 1982, *Jeremie 1023* (GH, P, US); Riviere du Vieux Fort, marecaga a 2 km de la mer, 06 Nov 1978, *Jeremie 610* (GH, NY, P). Sainte Rose, Morne Rouge, 03 Dec 1982, *Jeremie 1071* (P). W Morna a l'Eau, 30 May 1981, *Jeremie 918* (P); S de Sauvia, 08 Jun 1981, *Jeremie 942* (P). 1839, *Beaupertuis s.n.* (P); Dausme mare peres de la mu, Apr 1894, *Duss, 3441* (GH); *Duss 3637.3* (NY); 1932, *Gosier-Marcus, 589* (P); Entre Petit-Bourg et Goyave, marecage en arriere de la plage de Viard, 11 Dec 1982, *Jeremie 995* (GH, P); Grande-Terre, E. Ste Anne mare en arriere plage a Bois Jolan, 16 Nov 1983 *Jeremie 1331* (NY); 21 Mar 1935, *Quentin 917* (P); 0.7 km SSW of St. Louis, 03 Dec 1959, *Proctor 20243* (GH); 06 Jun 1935, *Quentin 939* (P); 18 Apr 1944, *Questel 4997* (P); Riviere de Vieux Fort, 2 km en amont de son embouchure, 02 Dec 1977, *Raynal 19615* (P [2 sheets]); Plage de la Grande Anse, 5 km N de Deshaies, 25 Jun 1975, *Raynal 15834* (P [2 sheets]); Port Louis, cote N de Grande Terre, en arriere de l'Anse lu Souffleur, 28 Jun 1975, *Raynal 15915* (P [2 sheets]); Port Louis, Grande Terre, 03 Apr 1936, *Stehle 674* (GH, P); 15 Nov 1962, *Stehle 8118* (P); 24 Mar 1936, *Stehle 673* (P [2 sheets]). **Dominica:** Portsmouth, between Prince Rupert Bay and Douglas Bay, 01 Aug 1938, *Hodge 267* (GH [2 sheets], NY); N Portsmouth, 18 Jul 1983, *Jeremie 1217* (GH, P). **Martinique:** Presqu'île de la Caravelle, 1883, *Duss 754* (C, NY). 1903, *Mouret 81* (P); without date, *Sieber s.n.* (M); Mar 1866, *Sieber s.n.* (P); et Guadeleupe, 1868, *Husnet 22* (P); without date, unknown but possibly an exchange sent to S. C. Correns from Sieber (M). **St. Lucia:** NE de Castries, Gros Islet, 22 Jan 1980, *Jeremie 827* (GH, P); Sulphur springs, 22 Jun 1975, *Raynal 15804* (P [2 sheets]); Anse Ger, 28 Jul 1985, *Slane 645* (GH); S of Micoud, 27 May 1986, *Slane 893* (GH); Cul de Sac, Mar 1968, *Sturrock 475* (GH). **Grenada:** Gosier, Grande Ravine, 30 Nov 1982, *Jeremie 1063* (GH, P); 30 Nov 1982, *Jeremie 1064* (GH, P). Near Queens Park, 18 Jul 1905, *Broadway 1784* (NY); 18 Jul 1905, *Broadway 1794* (GH); edge of Lake Grenada, 28 Mar 1977, *Howard 18928* (GH). **Barbados:** 1902, *Bovell 456* (NY); Gruene Hill Swamp, 08 Feb 1937, *Litosh & Allan 302* (P); **Christ Church:** Gruene Hill Swamp, 09 Nov 1996, *Rogers 96-128* (MICH); **St. George:** Dec 1889, *Eggers 6508* (P). **SOUTHERN NETHERLANDS ANTILLES: Curacao:** Museum garden, 10 Oct 1951, *Arnoldo 1675* (US). **ST. JAN:** Reef Bay, 02 Mar 1877, *Eggers s.n.* (C, GH). **Caribbean without location:** Jun 1887, *Eggers 440* (M, P); without date, *HB. Liebm.* (C).

SOUTH AMERICA. COLOMBIA: Departamento de Antioquia: approx. 1 km W of Turbo, 31 Mar 1962, *Feddema 2111* (MICH). **Departamento del Choco:** Bahia Solano Municipio, Corregimiento El Valle, 6° 21'N, 76° 26'W, 27 Apr 1989, *Espina et al. 3026* (CIIDIR). **Departamento del Magdalena:** Isla de Salamanca, km 20 de la carretera Cienaga-B, 10 Dec 1966, *Romero-Castaneda 10.507* (MO); Santa Marta, Sep 1898-1901, *Smith 245* (CM, E, MICH, NY, P, PH). **Providencia y Santa Catalina, Departamento de Archipielago de San Andres:** 22-27 Apr 1948, *Proctor 3267* (PH). Progreso, without date, *Gaumer 2402* (NY); El Valle, Buenaventura, 5-10 Oct 1922, *Killip 11744* (GH, NY, PH). **VENEZUELA: Territorio Federal Delta Amacuro:** mouth of Cano Guiniquina, between Punta Araguabisi and Punta Baja, at Barra Guiniquina, 9° 30'N, 60° 58'W, 18 Oct 1977, *Steyermark et al. 114913* (NY); between Ucupita and Las Mulas, 9° 3-5'N, 62° 00-04'W, 13 Oct 1977, *Steyermark et al. 114615* (NY). **Estado Falcon:** Carretera Yaracal-Araurima, a unos 6 km de la carr., Yaracal-Tucacas, 13 Feb 1981, *Cardozo 57* (NY); Parque Nacional Medanos de Coro, 4 km N del catedral de Coro, Canal de desague de Coro, y carca, 30 May 1980, *Wingfield 7770* (NY). **Estado Sucre:** Laguna Litorales de Cumana, 20 Jan 1974, *Campos 522* (K, NY, US); Cumana-Edo Sucre, 04 Sep 1972, *Guevara 508* (NY); El Penon, 19 Mar 1972, *Guevara 208* (NY); Laguna de patos Cumana Edo Sucre, 25 Aug 1972, *Guevara 429* (NY); Laguna La Bodega, inmediatamente al Este de Santa Fe., 17 Sep 1973, *Steyermark et al. 108552* (MO); Distrito Benitez, S of Guaraunos, 10° 32'5-33"N, 63° 7'W, 18 Feb 1980, *Steyermark et al. 121236* (NY). **Estado Zulia:** Dtto. Bolivar: km 6 de la via La Williams, desviando hacia el SO. en km. 30 de la carretera Lara-Zulia, 27 Aug 1983, *Hayward 253* (NY); 10 Nov 1922, *Pittier 10685* (GH, NY, P). Vicinity of Critstobal Colon, 05 Jan-22 Feb 1923, *Broadway 580* (GH, NY). **TRINIDAD:** 20 Nov 1921, *Britton 2466* (NY); Cedros, 1916, *Broadway 8551* (NY); Cedros Road, 71 1/4 mile, 26 Mar 1959, *Cowan and Foster 1323* (GH, NY, P); 26 Mar 1959, *Cowan and Foster 1325* (US); Ca. 2-3 miles E of Trinidad along the Beetham Hwy, 04 Aug 1970, *Davidse 2546* (MO, NY); Two miles S of the Churchill-Roosevelt Hwy along the Princess Margaret Hwy, 07 Aug 1970, *Davidse 2587* (NY); Pitch Lake, 24 May 1975, *Philcox 7790* (P); Nariva Swamp, W of M.P. 46, 12 Aug 1977, *Philcox & Ramcharan 8177* (NY); Caroni Swamp, pres de la route Port-of-Spain-San Fernando, env. 2 miles S de Caroni River, 28 May 1975, *Raynal 15579* (P); Pitch Lake, pres La Brea, 14 miles W de San Fernando, 24 May 1975, *Raynal 15536* (P). **TOBAGO:** Plymouth Road, 05 Oct 1909, *Broadway 3135* (Z); Buccoo Bay, 20 Apr 1939, *Elmore 510* (MICH). **GUYANA: Demerara-Mahaica Region:** East Coast Demerara, 11 Sep 1958, *Harrison 1533* (NY); Demerara, 05 Sep 1958, *Harrison 1520* (NY); East Coast, Demerara, 24 Sep 1958, *Harrison 1573* (K, NY); Georgetown, outskirts of the city, 31 Aug 1935, *Potter 542,* (GH [2 sheets]). **Pomeroon-Supenaam Region:** Moruka River, Mora Landing, 11 Aug 1921, *De La Cruz 941* (GH, NY, PH). Coast, 10 June 1888, *Jenman 4392* (NY); Jun 1890, *Jenman 6064* (NY); ca. 1888-1890, *Jenman 4092* (PH; mixed with *E. acutangula* from Paraguay). 23 Nov 1965, *Richard s.n.* (P [2 sheets]). **SURINAME: Distrikt Nickerie:** Nickerie, S side of Bigie-pan, 03 May 1949, *Lanjouw & Lindeman 3097a* (NY). 1891, *Krug 365* (PH); without date or specific location, *unknown* (NY). **FRENCH GUIANA: Departement de la Guyane:** Cayenne, Jan 1975, *Granville 2331* (P); 28 Feb 1976, *Raynal 18283* (P [2 sheets]); Cayenne, without date, *unknown* (P); Savans Sarcelle, entre la route Kourou-Mana et la mer, anv. 15 km a la E de Mana, 21 Mar 1976, *Raynal 18746* (P [2 sheets]); St Laurent, 06 Sep 1973, *Granville 1660* (P); Canton de Remire-Montjoly Zone du Degrad-des-Cannes 4^o 51N 52^o 17W, 13 Sep 2002, *Petitbon 586* (MO). 1838-1840, *Le Prieux s.n.* (P); 1836, *Ledrives 98* (P); 15 Dec 1956, *Lemme s.n.* (P); 1854, *Meliuor 13* (P); 17 May 1921, *Broadway 203* (GH, NY). **ECUADOR: Provincia de Esmeraldas:** km 102, Esmeraldas-La Tola, 27 Jul 1984, *Dodson et al. 14564* (MO). **Provincia de Galapagos: Albemarle Island:** 27 Jul 1977, *Adsersen 2234* (C); 5 miles NE of Webb Cove, 23 May 1932, *Howell 9459* (GH); Elizabeth Cove, 15 Feb 1899, *Snodgrass & Heller 261* (GH); Villamil 05 Mar 1906, *Stewart 1081* (GH, K, MO, NY, US). **Santa Cruz Island:** Tortuga Bay, 07 Sep 1965, *Knight 1023* (WIS); Academy Bay, 18 Feb 1964, *Fournier 249* (NY); Tortuga Bay, 04 Dec 1977, *Adsersen 1620* (C). **San Salvador Island:** Central South Bay, 08 May 1977, *Adsersen 1848* (C). **BRAZIL: Estado da Bahia:** Chapadao Ocidental da Bahia, 37 km N from Correntina, 44^o 47'W, 13^o 07'S, 29 Apr 1980, *Harley 21957* (NY); Piritiba, 11^o 43'S, 40^o 33'W, 30 Mar 1980, *Noblick 1857* (K); Col. Vale do Itapicuru, Jan 1951, *Pinto 753* (US); without date, *Salzman s.n.* (CGE [photo], E, FI [photo], MO, P). **Estado do Ceara:** Barra do Ceara, municipio de Fortalega, 25 Sep 1935, *Drouet 2503* (GH, MICH, NY); Erva, campo limpo, terreno alagado Campo dos Perizes, BR-135, km 27-28-MA, 19 Feb 1979, *Fernandes et al. 5601* (MO). **Estado de Mato Grosso do Sul:** Distrito Federal, Praia de Sernambetiba (Recreio dos Bandeirantes) 23^o 00'13"S, 43^o 20' 49"W, 04 Apr 1952, *Smith 6375* (MO, US). **Estado do Rio De Janeiro:** a beira da Lagoa de Marapendi Reserva Biologica, 11 Nov 1976, *Araujo 988* (NY); Fazenda da Sta Cruz, 09 Nov 1877, *Glaziou 9337* (C, NY); Cabo Frio, 01 May 1964, *Leao & Sick 29873* (M); Merity-sumpf, Dec 1911, *Luetzelburg 330* (M [mixed with *E. interstincta*], NY); Estado da Guanabara, 31 Oct 1969, *Sucre et al. 6163* (NY). **Estado de Santa Catarina:** Rio Travares, Ilha S Catarina, 23 Dec 1952, *Reitz 5097* (NY, US); **Estado de Sao Paulo:** Sebastianopolis, without date, *collector unknown 229* (E, GH, MO, NY, M); Peruibe, Estacao Ecologica Jureia-Itains, trilha para Cachoeira do Rio Verde, 08 Jan 1999, *Alves et al. 1793* (NY). **Estado de Sergipe:** Aracaju, Posto Paty BR 101, ca. 40 km N de aracaju, 21 Nov 1995, *Charudatan et al. 12* (NY). Without date, *Glaziou 510* (C, P); 09 Oct 1877, *Glaziou 9337* (P); Psrshybs (sic), Nov 1935, *Luetzelburg 26809* (M); 1821, *Riedel s.n.* (C, P). **PARAGUAY:** 08 Mar 1991, *Mereles 3973* (CIIDIR); without date, *Reugger s.n.* (ZT [2 sheets]), Paramarilo?, 1935, *Essed? 90* (NY).

AFRICA. ANGOLA: Moxico, Ikula hot springs by R. Zambezi, 17 Jan 1938, *Milne-Redhead 4195* (K, PRE). **CONGO:** Bas-Congo, 11 Sep 1913, *Bequaert 729* (PRE). **LIBERIA:** Crew town, Monrovia, 27 Jun 1909, *Massey 82* (NY). **PEMBA:** Makongwe Island, 16 Dec 1930, *Greenway 2730* (K). **SENEGAL:** Kaolak, 18 Oct 1953, *Berhaut 3794* (K); Ziguinchor, Km 54-57 Cap Skiring-Bignona, vicinity of Nyassia, 16^{o} 22'W, 12^{o} 29'N, 11 Sep 1994, *Laegaard et al. 16891* (K, US); Basse-Casamance, Fegroum, 08 Nov 1990, *Berghen 9301* (MO); Lyndiane, 30 Sep 1956, *Jacques-Georges 12460* (MO); 10 Apr 1946, *Roberty 6209* (Z). **SIERRA LEONE:** Rokupr, 03 Jul 1947, *Jordan 42* (K). **SOUTH AFRICA:** KwaZulu-Natal, North Coast, Lake Nhlabane area, E of North Lakevery, 28^{o} 36'S, 32^{o} 17'E, 23 Jan 1992, *Ward & Begg 11715* (NU). **TOGO:** Agwegan, 26 Jun 1985, *Schafer 8629* (MO, US).

APPENDIX III

ELEOCHARIS SPIRALIS SPECIMENS EXAMINED

ASIA. CHINA: Hainan: 25 Dec 1933, Liang 66592 (M, NY). Cheung Sheung, Hong Kong, 05 Dec 1969 Shiu Ying Hu 9036 (GH, MICH, US); Hong Kong, U Kai Sha, 16 Oct 1972, Shiu Ying Hu 12291 (GH). **INDIA:** Tranguebar, East Indies, without date, *Smith s.n.* (LIV); Indes Orient, without date, *unknown 725* (P). **MALAYSIA: Sabah:** British North Borneo, Mount Kinabula, Jesselton, 14-18 Dec 1915, Clemens 9716 (GH, K); W coast of Sabah, Kota Kinabalu, Likas Swamp Bird Sanctuary, 10 Dec 1996, *Azmi et al.,615* (K). Malesiana, without date, *unknown s.n.* (C). **PHILIPPINES: Luzon:** Manila and vicinity, Dec 1914, *Merrill 9788* (K, NY). **SRI LANKA: Amparai District:** Tandiadi Kalapu lagoon, S of Mile 215 on Rd. A 4, 07 Feb 1971, *Koyama et al. 14014* (GH, NY, US). **Eastern Province: Koddiyar Pattu District:** northern shore of Ullackalie lagoon, ca. 1.2 miles E of Toppur, 20 Feb 1971, *Koyama et al. 14060* (GH, NY). **THAILAND: Narathiwat:** Su Ngai Paadee, 28 Jun 1988, *Niyomdham 1874* (C, NY). Satiel (sic), 29 Dec 1927, *Kerr 13760* (K). **VIETNAM: Annam:** Nha Trang, 10 Sep 1922, *Poilane 4524* (P). **Dong Nai:** Tinh, Phu cuong, Jun 1967, *unknown 57* (P). Cochin China, 1862-1866, *Thorel 473* (K).

OCEANIA. AUSTRALIA: 1841, *Le Guillou s.n.* (P). **Northern Territory:** 12^o 40' S, 131^o 20' E, 14 Sep 1946, *Blake 16999* (BRI); Adelaide River, near Beatrice Hill, 09 Mar 1971, *Byrnes 2064* (BRI); Alice Springs, Beatrice Hill area, 12^o 38' S, 131^o 18'E, 01 Jul 1972, *Latz 3083* (BRI); Wessel Islands, 11^o 09' S, 136^o 44' E, 02 Oct 1972, *Latz 3394* (BRI); Darwin, Leanyer Swamp 12^o 21', 130^o 55', 28 Apr 1973, *Latz 3603* (BRI); 28 Apr 1973, *Latz 3606* (BRI); Darwin, Adelaide River floodplain, Arnhem Hwy, 12^o 41' S, 131^o 21' E, 17 Apr 1980, *Rankin 2255* (BRI); Imaluk Spring, Mandorah, 12.27^o S, 130.45^o E, 01 May 1988, *Russell-Smith & Lucas 5395* (BRI); Delissavile, Cox's Pen, 12^o 31' S, 130^o 44' E, 27 Mar 1948, *Specht 63* (BRI). **Queensland: Cook:** Cooktown, 24 May 1962, *Blake 21871* (BRI); 5 km ESE of Aurukun on track to Watson River, 03 Jun 1982, *Clarkson 4495* (BRI); ca 5 km ENE of the mouth of the MacDonald River, ca 68 k WNW of Heathlands, 18 Apr 1993, *Clarkson & Schultes 9905* (BRI); Annie River, Princes Charlotte Bay, 12 May 1979, *Elsol 728* (BRI); Water Day Creek, without date, *Fleche s.n.* (BRI); Welpa, Ooningan Nature Reserve, 01 Mar 1986, *Gunness 2019* (BRI); Skardon River Cape York in vicinity of Venture mining barge landing, 11 Apr 1994, *Gunness 2267* (BRI); O'Brien Road, W of Half Moon Creek wetland reserve, 19 Feb 1995, *Jago 3342* (BRI); Saibai Island, Torres Strait, May 1993, *Marks & Mackerras s.n.* (BRI); plains on E bank of Nomenade Creek, 19 Feb 1981, *Morto, 1128* (BRI); small swamp 0.5 km S of Luba Lake, 07 Apr 1992, *Neldner 3742* (BRI); Mt. Molloy, Cooktown Rd. about 6 km W of Mt Molly turn off, 17 Jun 1975, *Sharpe 1482* (BRI); Lizard Island, 17 Oct 1975, *Staples 2194* (BRI); Saibai Island, Torres Strait, 18 May 1999, *Waterhouse 5332* (BRI). **N Kennedy:** Gloucester Island, S end, 23 Apr 1994, *Batianoff et al. 940420G* (BRI); Cape Cleveland area, Bowling Green Bay Nat. Park, S of Townsville, 01 Jul 1991, *Bean 3388* (BRI); Thornley Park, 3 miles W of Townsville, 18 Jan 1962, *Blackman HL65* (BRI); Thornley Park, 3 miles W of Townsville, 14 Feb 1962, *Lavery HL99* (BRI); Town Common, Townsville, near Bald Rock, 28 Jun 1991, *Sharpe 5065* (BRI). **Port Curtis:** Gladstone, 10 Mar 1937, *Blake 12790* (BRI, K, NY); Stanage Bay, 19 Apr 1945, *Blake & Webb 15655* (BRI, K); 2 km E of Coowonga on road from Rockhampton to Emu Park, 05 May 1981, *Sharpe & Wilson 2754* (BRI). **S Kennedy:** Cape Gloucester, Shoal Beach Resort, 25 km E of Bowen, 20 Jul 1992, *Batianoff et al. 9207315* (BRI). **Wide Bay:** Woodgate, about 35 km E of Childers, 29 Apr 1977, *Sharpe & Dowling 2300* (BRI); Noosa Airport, close to edge of Lake Weijba, 09 Apr 1978, *Sharpe & Elsol 2323* (BRI); Lake Weyba, adjacent to Noosa Airport, Noosaville, 20 Dec 1975, *Swarbrick 6386* (BRI). 5.5 km SW of Emu Park on Rockhampton Rd, 05 May 1981, *Wilson 3666* (BRI). **NEW CALEDONIA:** 1868-1870, *Balansa 3095* (GH, P, Z); 1879?, *Hennecart s.n.* (P); Noumea, Baie Tina, 29 Dec 1971, *MacKee 24782* (P); without date, *unknown 3095* (GH). **PAPUA-NEW GUINEA: Morobe District:** Lae, T.N.G., 6^o 47 S, 147^o 00

E, 28 Nov 1963, *Womersley 19043* (GH [2 sheets]). Daru Island, Western Division, 06 Mar 1936, *Brass 6287* (BRI, GH); 5 miles NW of Hisiu village, Kairuku Subdistrict, Central District, Terr. of Papua, 17 Aug 1962, *Darbyshire 824* (BRI, K, GH).

APPENDIX IV

ELEOCHARIS ACUTANGULA SUBSP. *ACUTANGULA* SPECIMENS EXAMINED

NORTH AMERICA. MEXICO: Estado de Chiapas: large pond adjoining marsh with *Myrica*, *Vaccinium*, *Liquidambar*, and *Nyssa* on the eastern side of Pueblo Solistahuacan, Municipio of Pueblo Nuevo Solistahuacan, elev. 1700 m., 26 Oct 1971, *Breedlove 21527* (MO, NY). **Estado de Hidalgo:** boggy margin of Lake Atexca below Molango, 09 Nov 1946, *Moore 1938* (GH). **Estado de Jalisco:** swamps near Guadalajara, 1888, *Pringle 2061* (NY), swampy meadow ca. 5 miles east of Los Volcanes, road to Cuautla, in pine zone, elevation 1500 m, abundant, 20 Oct 1960, *McVaugh 20470* (MICH), Chamela, 19^{o}32'N, 105^{o}05'W, unpaved road along Rio Chamela, near grounds of the Instituto de Biologia of UNAM, alt. 60 m in small lagoon, 21 Apr 1980, *Rooden 716* (MEXU). **Estado de Nayarit:** near Lake Labor, ca 15 miles southeast of Tepic, flooded marshy meadows with *Sacciolepis, Leersia, Eleocharis, Canna,* elevation 1000m, abundant, often forming pure stands in water 30 cm deep, culms triangular, 25 Sep 1960, *McVaugh 19426* (MICH). **Estado de Tabasco:** hierba perenne en suelo humedo de sabana, depresion (prestamo) a la orilla del camino, km 64 rumbo de Huimanguillo a Fransisco Rueda, 35 msnm, 06 Nov 1979, *Orozco & Zamudio 2187* (MO). **Estado de Veracruz-Llave:** Orizabo, *Botteri 756* (GH), 4 km desviacion la Cienaga del Sur a Lerdo de Tejada, abundante , 16 Sep 1982, *Diego 3161* (MEXU), Orizaba, Botteri et Sumiehrast, Aug 1854, *unknown 189* (P). region de Orizaba, without date, *Bourgeau 2730* (P); Mpio. Las Choapas, ca 5.4 km S of the town of Las Choapas, along rural road to El Chichon and to Cerro del Nanchital, at the rancho Espiga de Oro, 13 Jul 2006, *Rosen et al. 3870* (CIIDIR, GH, K, MICH, MO, TAES, TEX, US, VSC, WIS). 1853, *Schlumberger 1367* (NY).

CENTRAL AMERICA. GUATEMALA: Departamento de Alta Verapaz: large swamp just E of Tactic, alt 1,300 m, 20 Feb 1942, *Steyermark 43970* (F), large swamp just E of Tactic, alt 1,450 m, 14 Apr 1941, *Standley 92380* (F), cutover and second-growth forest along valley 1-5 km E of San Juan Chamelco, 15^{o}25'N, 90^{o}15'W, alt. 1,500-1,600 m, 01 Feb 1969, *Williams et al. 40445* (F [2 sheets]). **Departamento de Chiquimula:** between Chiquimula and La Laguna, alt. 500-1000 m, 27 Oct 1939, *Steyermark 30713* (F). **Departamento de Huehuetenango,** vicinity of Maxbal, about 17 miles N of Barillas, Sierra de los Cuchumatanes, alt. 1500 m, 15-16 Jul 1942, *Steyermark 48770* (F), between San Sebastian H. and large penasco above town, alt. 2,000-2,200 m, around laguna de Peol, 13 Aug 1942, *Steyermark 50522* (F). **Departamento de Izabal:** near Puerto Barrios, sea level, 25 Apr-06 May 1939, *Standley 72862* (F). **Departamento de Jutiapa:** SE end of Potrero Carrillo, 13 miles NE of Jalapa, alt. 1500-1700 m, spongy ground of laguna, 12 Dec 1939, *Steyermark 33099* (F), El Barrial, E of Jutiapa, alt. 800 m, 30 Oct 1940, *Standley 75780* (F), Lago Retana, between Ovejero and Progresso, 26 Nov 1939, *Steyermark 31991* (NY; mixed with *E. mitrata* [Griseb.] C. B. Clarke). **Departamento de Santa Rosa:** dried lake bed of Lagunata Junquilla, old crater lake 4 miles N of Barberena, 18 Feb 1951, *Fassett 28844* (F), Lago de los Pinos, near Sabanetas, 20 Dec 1938, *Standley 60439* (F). **Departmento de Izabal:** Coabn, alt. 4300 pp., Jul 1887, *Tuerckheim 1283* (GH, NY, US), vicinity of Puerto Barrios, at sea level, 2-6 Jun 1922, *Standley 25150* (GH, NY, US), Cristina, 22 May 1919, *Blake 7587* (US), between Milla 49.5 and Cristina, alt. 65-70 m, in prairie with pines, 30 Mar 1940, *Steyermark 38415* (F). **BELIZE:** Toledo District: near junction of Southern Highway and Pine Hill. Rhizomatous, culms erect, sharply 3-angled; forming dense stands in open pond, 22 Nov 1998, *Holst et al. 7064* (MO). **HONDURAS: Departamento de Comayagua:** vicinity of Siguatepeque, about 1050 m, in ditch on plain, 25 Mar-05 Apr 1947, *Standley & Chacon 6595* (F), in marsh near Siguatepeque, 1050 m alt., 9 Jul 1936, *Yuncker et al. 5760* (MICH). **Departamento de Copan:** wet fields and thickets in draw with pine forest on higher ground, 14 Jul 1971, *Harmon & Fuentes 6445* (MO, NY [2 sheets]). **Departmento de Francisco Morazan:**

near Las Mesas, 900 m, small open bog, mostly in shallow water, 10 Sep 1950, *Standley 26634* (GH). **Departamento de Olancho:** Santa Maria del Carbon, 23 mi NE of San Esteban along road to Bonito Oriental, marsh in pine forest dominated by *Eriochrysis*, *Rhynchospora*, *Eleocharis, and* Cyperus*,* 15^o 26' 24" N, 85^o 34' 57" W , 03 Jul 1994, *Davidse et al. 35564* (CIIDIR). **EL SALVADOR: Departamento de Ahuachapan:** shallow water, Lagunita las Ninfas, Apaneca, 28 Jan 1951, *Fassett 28721* (GH). in shallow water, Laguna Verde, Apaneca, 30 Dec 1950, *Fassett 28526* (F [2 sheets], WIS), shallow water, Lagunita las Ninfas, Apaneca, 28 Jan 1951, *Fassett 28721* (F [2 sheets], MICH, WIS), Lago de Ninfas, Cordillera de Grande de Apaneca; north-west of Juayua, 84^{o}47'55W, 13^{o}52'29N, alt. 1600 m, marsh filled volcanic crater surrounded by broadleaf forest., 06 Feb 1998, *Davidse et al. 37366* (MEXU, MO). **NICARUAGRA: Comarca del Cabo:** Bihmona, along creek, 7 Jul 1972, *Seymor 5707* (CIIDIR, GH, MO, mixed with *E. interstincta*). **Departamento de Esteli :** Reserva Natural Miraflor, Municipio de Esteli, Comunidad los Volcancitos, aquatica, 13^{o}10'N, 086^{o}12'W, 10 Jul 1999, *Rueda et al. 11643* (MO), 1.5 km al S del Plan Helado, camino a Miraflor; 13o13'N, 86o15'W, elev. Approx. 1300 m. Inflorescencia cafe., 23 Oct 1983, *Moreno 22399* (CIIDIR, MO), Mesas Moropotente, *Typha* marsh in cattle watering pond in oak forest, 13^o 14'N, 86^o 18' W, 29 May 1985, *Davidse et al. 30629* (CIIDIR, MO). **Departamento de Zelaya:** Cano Manso Awalka Tingni, reached by Geodesia turn on road between Torre 7 and Bismuna Tara, ca. 11.9 km SW of Bismuna Tarra, savanna, tall graminoids and shrubs immediately aong cano, with silt sand soil, 14^o 41' N, 83^o 30'W, 19 Apr 1978, *Stevens 7704* (CIIDIR [2 sheets]), Cano Manso Awalka Tingni, reached by Geodesia turn on road between Torre 7 and Bismuna Tara, ca. 11.9 km SW of Bismuna Tarra, savanna, tall graminoids and shrubs immediately along cano, with silt sand soil, 14^o 41' N, 83^o 30'W, 19 Apr 1978, *Stevens 7704* (MO). **COSTA RICA: Isla De Cocos:** Macollas en suelo humedo, a la orilla del par tano, Bahia de Wafer, ca. nivel del mar, 31 Jul 1981, *Gomez-Laurito 6915* (F, MO). **Provincia de Alajuela:** 6 km W of Venicia, elev. 450 m, small marsh among pastures, 15 Oct 1968, *Davidse & Pohl 1307* (F, MO), Laguna Fraijanes, ca. 12 km N of city of Alajuela, 07 Aug 1987, *Crow & Rivera 7007* (MO), 07 Mar 1937, *Quiros 643* (F), Los Chiles, area palustre en el Rio Frio, cercana al muelle, 11^{o}01'50"N, 42^{o}43'18"W, macollas en lodo, 15 Dec 1993, *Gomez-Laurito et al. 12551* (F). **Provincia de Cartago :** Laguna Dona Anacleta, Canton Paraiso, Lago Crater, 22 Aug 1983, *Novelo 1209* (MO), Rio Reventazon, Catie agriculture station, Turriabla, mostly near nature trail, 12 Jan 1987, *Hill et al. 17731* (NY), Las Concavas, 1400 m, 27 Feb 1924, *Standley 35979* (US), along the Rio Reventado, N of Cartago, 26 Feb 1926, *Standley & Valerio 49419* (F, US). **Provincia de Guanacaste:** open, virtually treeless marshy area at upper N fork of Rio Sabalito, just N of San Joaquin de Coto Brus, 8^o 49.5' N, 82^o 57' W, common in innundated sites at margin of marshy lake, 13 Sep 1985, *Grayum et al. 6011* (MO), Santa Rosa National Park, Laguna Escondida, small shallow pond, dam at outlet, which dries in dry season, frequent, emergent, fruits mostly disarticulated, 02 Nov 1984, *Crow & Rivera 6121* (MO), ca. 200 m from Interamerican Hwy. on road to Cuajinquil (10 m N of Santa Rosa at. Park), temp. pond on S side of road, water almost dried up, 16 Nov 1984, *Crow 6222* (F, MO), Canton de La Cruz, ca. 5 km from road to Santa Cecilia, very shallow pond on S side of road, forming large patches, very abundant, 11^o 01' 20" N, 85^o 32' 30" W, 27 Aug 1990, *Crow & Rivera 7633* (F, MO), intersecton of interamerican Hwy. and road to Murcielago, marsh dominated by Eleocharis spp., 26 Jan 1983, *Davidse et al. 23280* (MO), Lagunas Coyol y Guayabal, La Cruz, Guanacaste, elev. 250 m, 24 Nov 1982, *Gomez-Laurito 9157* (F). **Provincia de Puntarenas:** San Joachim de Sabosa, just N of San Vito, small marsh along road recently formed during road construction, 22 Feb 1982, *Barringer & Gomez 1688* (F), airport just N of San Vito, ca. 1000 m, roadside pond with marshy margins, growing in 25 cm of water, 23 Sep 1984, *Davidse & Herrera 29432* (GA, NY, USF, WIS, MO). **PANAMA: Provincia de Chiriqui:** wet meadow S of El Boquete, 01 Mar 1918, *Killip 4569* (NY), foothills, vicinity of El Boquete, 1000-1300 m, 07 Oct 1911, *Hitchcock 8263* (US). **Provincia De Cocle:** El Valle de Anton and vicinity, 500-700 m, 23-27 Jul 1935, *Seibert 476* (MO, NY, US), between Las Margaritas and El Valle, found in bog, Jul 15-Aug 8 1938, *Woodson et al. 1720* (GH, MO, NY), Aguadulce, near sea level, 3-6 Dec 1911, *Pittier 4928* (US). **Provincia de Veraguas:**

vicinity of La Mesa in sunny muddy bottom in pasture, 28 Dec 1968, *Tyson 6054* (MO). Amerique Meridionale, *Bolive 138* (P).

CARIBEAN BASIN. JAMAICA: Clarendon Parish: Mason River Field Station, 4 mi W of Kellitts, 2300 m, wet savanna, 27-29 Jul 1979, *Thomas 2146* (MICH), Mason River savanna W fo Kellits, 16 Jul 1962, *Fosberg 42755* (NY). **Saint Catherine Parish:** Charlton, near Ewarton, 03 Apr 1903, *Harris 8513* (NY), river head near Ewarton, 03 Apr 1903, *Underwood s.n.* (NY). **DOMINICA REPUBLIC: San Cristóbal province:** in mud near stream in arroyo between Duarte Hwy. Kl. 28 and Haina, 11 Oct 1947, *Allard 15976* (GH). **Santa Domingo Province:** 8 km from La Batata on road to Mata de Piedra and La Catalina, 09 Dec 1980, *Mejia & Zanoni 9753* (NY), en una laguna, Mata de Palma, Guerra, 08 Oct 1975, *Liogier & Melo 24010* (NY). **DOMINICA:** Lesser Antilles, St. George Parish, vicinity of freshwater lake, dwarfed cloudforest on ridges, cool wet area, NE of Laudat, E side of Morne Macaque, loccaly common, 2500', 20 Mar 1991, *Hill et al. 22119* (GH, NY). **GRENADA:** Nelle Grenade, 1844, *Goudot s.n.* (P), New Grenada, <1892, *Triana s.n.* (E), Nouvelle-Grenade, Prov. De Charo, 1851-1857, collector unknown *420* (P).

SOUTH AMERICA. COLOMBIA: Departamento de Antioquia: Municipio Valdivia, Corregimiento de Puerto Valdivia, km 11 de Pto Valdivia, mina de Oro "Canarias", colecciones en escombreras de 2 anos, 7° 25' N, 75° 26' O, 14 May 1987, *Callejas et al. 3486* (MO [2 sheets], NY), Mpio., Guatape, road to San Rafael ca. 4 km E of Guatape-Santa Rita road (Finca Montepinar), secondary forest and wetland ca 1 km N of road, 06°15'N, 75° 08' W, 22 Oct 1987, *Brant & Roldan 1461* (MO), Rio Negro, 2100 m, swampy soil, 27 Jul 1930, *Archer 477* (US), El Bordo, near Frontino, 1500 m, 27 Mar 1944, *Core 483* (NY, US), Hacienda El Darien, 150 m snm Carretera Mutata-Pavarando, Municipio Mutata, 07 Mar 1987, *Fonnegra et al. 1830* (MO). **Departamento de Risaralda:** hacienda Alejandria km 6 carretera La Virginia-Cerrito, extremo norte de parte ancha del Valle del Rio Cauca, lomas bajas, 22 Aug 1989, *Silverstone-Sopkin 5504* (MO). **Departamento del Cauca:** Chisquio, Finca Los Derrumbos, alt. c. 1700 m, marsh, 11 May 1940, *Asplund 10577* (LL), Rio Sucio to Rio Piedras, W of Popayan, 03 Jul 1922, *Pennell & Killip 8241* (NY). **Departamento del Huila:** marshy ditch, 3 km W of Garzon, upper basin of Rio Magdalena, 17 Feb 1959, *Mason 13888* (GH, US). **Departamento del Meta:** about 17 km SW of Puerto Lopez, margin of shallow wet depression along road between La Balsa and Bocas del Guayuriba, 17 Jan 1970, *Schuyler 4165* (PH). **Departamento del Valle del Cauca:** Calima, on Rio Calima, 14-15 Sep 1922, *Killip 11247* (GH, NY, PH). Agua Sucia, rives du torrent agua sucia, 1800 m, without date, *Langlasse 87* (GH, P, US). Prov. De Chois, Mar 1833, *Triano s.n.* (US). Papayan, 1700-2000 m, without date, *Lehmann? 8432* (F, GH). **VENEZUELA: Estado Apure :** Guanare, Esteros y pantanos cerca de los diques y el cano Matorral, 7° 30' Lat. N, 69° 30' Long O., 25 Oct 1980, *Stergios 2387* (MO). **Estado Aragua:** El Limon, near Maracay, in Morass, 29 Jan 1922, *Pittier 10116* (GH). **Estado Bolivar:** Gran Sabana, Hato Sta. Teresa, Mar 1946, *Tamayo 3211* (F, US), Gran Sabana, Ubicacion, Bolivar, municipio Gran Sabana, 20 Jul 1987, *Duno & Teran 85* (NY). **Estado Guarico:** Orituco, 25 km SW de la Estacion Biologice de la Clanus (sic) Edo Gcarico, 19 Sep 1982, *Montes 1343* (MO), Dtto: Infante, Parque Nacional Aguaro-Guariquito, Morichal Indio Viejo, Dec 1981, *Delascio et al. 11566* (MO), Sabanas de Juan Paulino, via Los Arroyuelos, Dec 1981, *Delascio et al. 11099* (MO). **Estado Portuguesa:** terrenos de la Unellez 9°4"N, 69° 49" O, 06 Sep 1984, *Stergios 7051* (MO), Sistema de riego "Las Majaguas" presa 1-2-3, sector Agua Blanca, 18 Jul 1972, *Trujillo 11180* (NY). Estero del Rio Oritico, 25 km Sur de La Estacion Biologicle, 17 Jun 1982, *Montes 1118* (MO). Savanes marecageuses du Guaritico, 22 May 1896, *Geay 1894* (P). **GUYANA: Upper Takutu-Upper Essequibo Region:** Rupununi Distr., Shea Village, savanna along creek, 09 Feb 1994, *Jansen-Jacobs et al. 3634* (NY, US), Rupununi Distr., savanna in pond, 03 Aug 1995, *Jansen-Jacobs et al. 4744* (K, NY), South Rupununi, Toot River, 40 km SE Aishalton village along Marudi Road, tall mesic forest, in wet depressions, 02° 15' N, 59° 10' W, 26 Apr 1994, *Henkel & James 3769* (MO, NY), South Rupununi savanna, Aishalton village, palm swamp, 02° 31' N, 59° 20' W, 03 Aug 1993, *Henkel & James 3976* (MO, NY). **SURINAM:**

in Maurisie swamp, W of 4-Gebroeders Mts., 27 Sep 1968, *Oldenberger et al. 194* (NY). **ECUADOR: Provincia de Napo:** Amazonica, Archidona, Coca km 9.3 roadside, 77° 45' W, 00° 45' S, 15 Apr 1988, *Laegaard & Renvoize 70909* (MO, NY). **Provincia del Pastaza:** Amazonica, Hacienda San Antonio de Baron von Humboldt, 2 km al Nede Mera, 1° 27' S, 78° 06' W, 20 Feb-20 Mar 1985, *Palacios et al. 144* (MO), Amazonica, Mera, marsh in rastrojo, alt. c. 1100 m., 13 Dec 1955, *Asplund 18831* (K, NY, US, Z). **BRAZIL: Distrito Federal:** Brasilia, area de inundacao da Bar ragem do Sao Bartolomeu, 27 Jun 1979, *Heringer 1652* (NY). **Estado da Bahia:** 37 km N from Correntina, on the Inhaumas road, 29 Apr 1980, *Harley 21957* (NY). **Estado de Mato Grosso:** in very marshy ground at margin of small lake, 17 Oct 1968, *Harley et al. 10711* (NY), Rodovia de Miranda a Campao, 15 Dec 1976, *Shepherd et al. H090* (E). **Estado de Minas Gerais:** without location, 1816-1821, *Catal 616* (K, P), ca. 10 km of the Rio Doce at Governador Valadares, *Typha* marsh, 28 Mar 1976, *Davidse et al. 11,466* (MO, NY), 21 km N of Medina along Hwy. BR-116, marsh with open water in center and grassy margin, 30 Mar 1976, *Davidse 11,595* (MO, NY), road between Varginha to Eloi Mendas, open swampy by road, forming large comunities, 07 Feb 1970, *Koyama et al. 13704* (CIIDIR, MICH). **Estado de Sao Paulo:** Butantan, S. Paulo, without date, *Gehrt 5403* (GH, NY), Rio Claro, 05 Jul 2003, *Vanzela 35.428* (CIIDIR), near Cargo do Meio, municipio de Tanabi, 50 km NW from Sao Jose do Rio Preto, open swampy ground, 22 Nov 1987, *Tsugaru & Oyama 2176* (NY), road between Pres. Prudente and Pres. Bernardes, in shallow water with *Fuirena*, 22 Feb 1970, *Koyama et al. 13760* (NY). **Estado do Amazonas:** lagoa permanente, 500 m ao Sul da BR 230 km 4, 15 Aug 1980, *Janssen & Gemtchujnicov 514* (M); lagoa permanente, 500 m ao Noreste da BR 230 km 7, 20 Aug 1980, *Janssen & Gemtchujnicov 526* (M). **Estado do Maranhao:** Brejo, Ets. Ecologica UFMG, 02 Apr 1991, *Neto 461* (CIIDIR). **Estado do Parana:** Rolandia, Fazenda Conquista, area alagada, dentro da lagoa, no. 14, 11 Mar 2003, *Vanzela 35.42* (CIIDIR), Sapopema, 05 Jul 2003, *Silva 35.436* (CIIDIR), 5 km N of Curitiba, artificial pool near chacara of Nowacki near Barreirinha, 12 Jan 1967, *Lindeman & Haas 4030* (NY). **Estado do Rio de Janeiro:** Goias, Formosa, Bisual, 20 Oct 1965, *Pereira & Duarte 9414* (NY). **Estado do Rio Grande do Norte:** near Bento Fernandes, 70 km W from Natal, shallow at pond's edge, 28 Aug 1987, *Tsugaru & Sano B-1273* (GH). **Estado do Rio Grande do Sul:** M. Rio Pardo, Riniao Reserva, Feb 1923, *Jurgens s.n.* (US). Without location, 1844, *Weddele 1195* (P), *Warming? 18/564* (P). **BOLIVIA: Departamento de La Paz :** Iturralde, Luisita, sabana humeda, W del rio Beni, Palmar, 12 Sep 1984, *Haase 540* (NY), Apolo, 27 Feb 1902, *Williams 916* (NY). **Departamento de Santa Cruz:** Andres Ibanez, NE side of Viru-Viru Pampa and property of Aeropuerto Internacional, along road to Chuchio, 4.5 km E of turnoff from highway from Santa Cruz to Warnes on road to Chuchio, 17°37'S, 63°07W, sandy area, former grassland with patches of small trees, around pond, forming a dense colony at edge of pond, stems sharply triangular, almost winged, 15 May 1998, *Nee 49365* (CIIDIR, TEX), Andres Ichilo, N of Buena Vista, N end of Laguna Madrejon ("Laguna Candelaria" on topographic map), shallow lake, open water 10 years ago, now mostly filled with aquatic vegetation, *Eichhornia*, *Sagittaria*, Cyperaceae, *Aeschynomene* spp., surrounded by savanna woodlands on sandy soils, 17°23'S, 63°40'W, alt. 295 m. , 31 Oct 1990, *Nee 39625* (MO, TEX), Nuflo de Chavez, Concepcion, wetland ca. 0.5 km NE of Concepcion, rare, growing in shallow water along the edge of the system, 04 Dec 1996, *Ritter 3939* (MO), Velasco, the road to San Ignacio, ca. 5 km W of Santa Rosa de la Roca, very abundant, 15°53'33"S, 61°31'0"W, 19 Jun 1998, *Ritter et al. 4255* (MO), Nuflo de Chavez, Est. Santa Maria, 5 km S of Concepcion, mosaic of semideciduous forest, wooded savanna, and savanna wetland, 21 Jan 1986, *Killeen 1650* (F, US), Nuflo de Chavez, Est. La Pachanga, 5 km S of Concepcion, 16°08'S, 62°05W, 500 m, eroded tertiary plantation surface overlying precambrian shield, mosaic of semideciduous forest, wooded savanna, and savanna wetland, common, 26 Nov 1986, *Killeen 2248* (F), Del Sara, Buena vista, 450 m, 25 Mar 1916, *Steinbach 9754* (GH). **PARAGUAY: Departamento Central:** Estero del Ypoa, Villeta, Puerto Guyrati, 4.5 km S of Villeta, inundated savanna on clay soil, 25° 33' S, 57° 32' W, 02 Dec 1992, *Zardini & Aquino 34134* (CIIDIR, US), Estero del Ypoa, 15 km SW of Nueva Italia, Coast in from Isla Guazu, innundated savanna, 27° 45' S, 057° 32' W, 07 Dec 1990, *Zardini & Velazquez 24808* (MO), Estero del Ypoa, 10 km SW of Nueva Italia, S of

Canada, 1 km from the coast, inundated savanna, 25^{o} 20' S, 057^{o} 28' W, 07 Dec 1990, *Zardini & Salinas 24986* (MO), between Nueva Italia and Yuquyty on a hill, inundated savanna, 25^{o}37'S 57^{o}26'W, 08 Dec 1990, *Zardini & Velazquez 25076* (MO), Arroyo Yuquyty, 7 km E of Nueva Italia, inundated savanna, 25^{o}36'S, 057^{o}25'W, herb 80 cm, 8 Dec 1990, *Zardini & Velazquez 25156* (MO), Estero Ypoa, between Nueva Italia and Yuquyty on a hill, innundated savanna, 25^{o}37'S 57^{o}26'W, 18 Mar 1992, *Zardini & Aquino 31333* (MICH). **Departamento de Caazapa:** Tavai, Enrramadita, hierba palustre, flores verdosas, en el estero, 05 Dec 1988, *Mereles 2067*, *2069*, *2070*, *2081* (MO), Zovai, Estero Bogado, hierba palustre, Dec 1988, *Mereles 2080* (MO). **Departamento de la Cordillera:** 1 km E of Nueva Colombia on road to Atyra, on a hill, inundated savanna, 25^{o} 10'S, 057^{o} 13' W, 09 Jun 1990, *Zardini & Velazquez 20917* (MO), Estero del Ypoa, 10 km SW of Nueva Italia, S of Canada, inundated savanna, 25^{o}20'S, 057^{o}28'W, 10 Feb 1990, *Zardini & Velazquez 18952* (MO), Ypoa, 13 km SW of Nueva Italia, NW of Pindoty, innundated savanna, 25^{o} 20'S, 57^{o} 28'W, 27 Jan 1990, *Zardini & Velazquez 18551* (MO). **Departamento de Misiones:** Estancia La Soledad, Santiago, swamp, 30 Apr 1961, *Pedersen 6029* (US, GH, MO, NY, TEX). **Departamento de Paraguari:** Estero Ypoa, between Nueva Italia and Yuquyty on a hill, innundated savanna, 25^{o}37'S, 57^{o}26'W, 18 Mar 1992, *Zardini & Aquino 31333* (CIIDIR). **Departamento del Amambay:** Ao. Estrella, Prop. De Heisecke, 22^{o} 20'S, 56^{o}20'W, flores cremosas, orillas de tajamares, suelo humedo, 08 May 1989, *Soria 3749* (MO). Central Paraguay, 1889, *Morong 298* (NY), Central Paraguay, 1888-1890, *Morong 499* (F, MO, NY [2 sheets], PH [mixed with E. mutata from British Guiana]). Without location, 11 Nov 1874, *Balansa 678* (P), Nov (1885-1895), *Hassler 1482* (P), Depto. Eaazopa, Zoval, 05 Dec 1988, *Mereles 2389* (MO), 1928, *Jorgensen 4497* (F, MO, NY, PH, US [2 sheets]), Zwischen Rio Apa und Rio Aquidaban, 1908-1909, *Fiebrig 5349* (E), Zwischen Rio Apa und Rio Aquidaban, 1908-1909, *Fiebrig 5349* (E), Zwischen Rio Apa und Rio Aquidaban, 1908-1909, *Fiebrig 5349* (GH, M, P), Sierra de Maracayu, in regione vicine "Igatimi", without date, *Hassler 5676* (GH, NY, P), in regione fluminis Alto Parana, 1909-10, *Fiebrig 6148* (US), in regione collium, Cerros de Tobaty, 1900, *Hassler 6414* (GH, NY, P), in regione collium: Cordillera de Villa-Rica, 1905, *Hassler 8589* (GH, MO), in regione collium: Cordillera de Villa-Rica, 1905, *Hassler 8589* (NY, P). **ARGENTENA: Provincia de Corrientes:** Concepcion, Carambola, Estancis "Buena Vista", very wet ground & shallow water, 19 Feb 1985, *Pedersen 14072* (MO, NY), Santo Tome, Estancia Garruchos, potrero Curuzu, en pantano, 7 Nov 1972, *Krapovickas et al. 21255* (ZT), Santo Tome, Estancia Garruchos, potrero Curuzu, en pantano, 30 Mar 1974, *Krapovickas et al. 24625* (ZT), Dep. Santo Tome, Ruta 1, Galarza, Reserva Natural Provincial del Ibera, Laguna Galarza, en embalsado, costa sureste de la laguna, 27 Apr 1995, *Arbo et al, 6644* (GH). **Provincia de Misiones,** Sausta Aira, 1913, *Rodriguez 763* (GH), Apostoles, ruta 14, 10 km al N de San Jose, banado acido, 22 Jan 1983, *Guaglianone et al. 867* (MO), Posadas, pr. Praedium "La Spranja" in fossa non profunda, 17 Dec 1907, *Ekman 1295* (MO, NY), Posadas, Santa Ines, 08 Feb 1924, *Parosi 630* (F). **Provincia del Chaco :** Dep 1o de Mayo, Colonia Benitez, embalsado burger, 16 Dec 1943, *Schulz 4118* (F, GH). Rio Santa Lucia, 31 Jan 1949, *Pedersen 207* (US), Estancia, Santa Teresa, Canada Portillo, in shallow water, 17 Dec 1954, *Pedersen 3054* (MO, NY, US [2 sheets]).

AFRICA. ANGOLA: Provincia de Benguela: Gebirge sudlich Ganda, Tumpel bei Calusipa, 30 km sudlich Chicuma, 1580 m, 24 Dec 1951, *Hess 51/419* (Z). **Provincia do Bie Bie:** Baixo Cubango, 28 km nordlich Caiundo in der Umgebung der Missao cat. Capico, flacher sumpf, 31 Jan 1952, *Hess 52/525* (Z). **BOTSWANA: Ngamiland District:** Moremi Wildlife Reserve, N Okavango swamp, Kwani River floodplain, common sedge up to 3'6" in swamp, forms pure stands, Jul 1964, *Tinley 1057* (NU). Northern, last two miles of the Santantadibe River, before it joins the Thamalakane River, 09 Apr 1972, *Smith 202* (K, NU, PRE). Okavango, 500 m, upstream Gobega lagoon, along edge of fast flowing river, 11 Apr 1984, *Ellery 174A* (PRE). In 1-1.5 m water, 01 Mar 1972, *Russell & Biegel 1484* (MO [2 sheets]). **BURKINA FASO: Province de l' Oudalan:** Mare de Bidi, large seasonally inundated swamp with aquatic plants, 20 Sep 1996, *Madsen 5749* (NY). **Province du Boulgou:** some km SE of Tenkodogo, waterhole with *Oryza* and other aquatic plants, 31 Aug 1996, *Madsen 5455* (NY). **BURUNDI:**

iProvense ya Bubanza: Plaine Rusizi km 14, sevana palmaraie marais, 800 m, 16 Mar 1975, *Reekmans 4390* (MO), plaine Rusizi km 14 marais a Oriza longistaminata, helophyte en grosses touffes, 11 Apr 1981, *Reekmans 9990* (MO). **Provense ya Bujumbura:** Bujumbura, plaine Rusizi km 14, savane palmeraie, 780 m, 13 Feb 1972, *Reekmans 1539* (MO). **iProvense ya Bururi:** Gihofi-Gihara, marais a *Nymphaea*, 20 May 1980, *Reekmans 9205* (MO). Plaine de le Rusizi Rukoko, 08 Mar 1987, *Caljon 3045* (MO, WIS). Kiofi swamp, Sep 24 1972, *Rammeloo 4846* (MO). **CAMEROON: Province du Nord:** about 15 km NE of Maroua, along road to Waza, moist savanna, clay soil, 12 Sep 1964, *Wilde 3215* (K). **CENTRAL AFRICAN REPUBLIC: Prefecture de la Sangha-Mbaere:** Sangha Economique, Dzanga-Sangha Reserve, 40 km S of Lidjombo on tributary of Keine, sedge clearing in lowland forest along permanently flowing streram, 02^{o}24'N, 16^{o}09'E, 26 Oct 1988, *Harris & Fay 1488* (MO, PRE). **COMORO ISLANDS:** Mayotte, Grande Terre, Ouangani, Coconi, Valarana, plante aquatique a tige a section triangulaire et creuse, 26 Fev 2002, *Barthelat & Sifari 708* (P). **CONGO:** Vallie Uruanda, 26 Oct 1953, *Liben 852* (K, PRE), Kiofi, 19 Feb 1952, *Reed 1189* (NY). **ETHIOPIA: Kaffa Province:** Kochi, about 5 km E of Jimma, along the road to Addis Ababa, 02 Nov 1970, *Friis et al. 38* (C, K), about 10 km WSW of Jimma, along road to Bouga, marshy land along rivulet, 10 VIIX 1965, *Raynal 1971* (MO), about 10 km SW of Jimma, along road to Bonga, 10 Aug 1965, *Wilde et al. 7565* (C). Shoa, ca. 4 km S of Thibe, swampy grasland, 19 Sep 1975, *Gilbert & Thulin 887* (K). **GABON: Province de la Nyanga :** a plus ou moins 7km sur la route de Doussala vers Bongo dans la direction Nord-Ouest, Petit etang, 2^{o} 19'S, 10^{o} 33' E, 25 Mar 2000, *Sosef 1016* (MO). **Province du Haut-Ogooue :** Bateke Plateau, Mpassa River watershed, 4.2 km N of station of the Project de Protection des Gorilles, wet savanna, 27 Nov 2001, *Walters et al. 982* (MO). **GHANA: Brong-Ahafo Region:** 1 m S of Atebubu, growing in shallow water at the edge of a pond, 16 Nov 1970, *Hall & Duodu 42128* (MO). **GUINEA-BISSAU:** 08 Dec 1944, *unknown 1594* (MO). **IVORY COAST: Departement d' Abidjan:** coast savanna, near the airport of Abidjan, 21 Oct 1963, *Wilde 1109* (Z). **LIBERIA: Grand Bassa County:** Sanokwele District, Ganta, 02 Dec 1935, *Harley 781* (NY, US). **Nimba County:** Mt. Nimba, Crete, Marc a', 04 Jul 1974, *Adam 28878* (MO). **MADAGASCAR: Antananarivo Province :** Ankazobe, Jun 1927, *Bathie 17929* (P, US). **Fianarantsoa Province:** Ambatofinandrahana, Itremo, petite vallee a l'ouest du Massif de l'itremo, 1680 m, 20^{o}37'22"S, 46^{o}33'15"E, vegetation aquatique dans petit ruisseau, 26 Nov 1993, *Du Puy & Andriantiana 2429* (MO, K, P). **Mahajanga province :** 10 km E Antsalova, 20 Mar 1993, *Villiers et al. 4855* (K). **Toamasina province,** Marais de Didy, voir Joncacee de a a 2m, 21 Feb 1943, *Cours 1758* (P). Without location, 1963, *Bosser 17.567* (MO, P), 1913, *Bathie 2722* (P), *Bathie 4572* (P), 1903, *Bathie 7139* (P), Nae Kely, Ankaratia, 1956, *Bosser 8919* (P, MO), Nov 1926, *Bathie 11922* (P), 1921, *Bathie 14244* (P), *Bathie 14568* (P), 1897, *Baron s.n.* (P), 12 Nov 1921, *Decary s.n.* (P), les marais, *Poiret s.n.* (P), Tsarasaotra, Dec 1897, *Bathie 418* (P). **MALAWI: Central Region:** Kasungu National Park, Angombe Hill, waterhole-spring, rare, 03 Sep 1970, *Hall-Martin 1712* (PRE). **NIGERIA: Kano:** edge of wet hallow in water, 12 Sep 1973, *Jackson & Apcjoye 10-12973* (MO). **Plateau:** in vicinity of Bukuru, near Jos, 29 Jun 1970, *Blum 2488* (WIS). **RHODESIA: Hartley:** Avondale farm dam, 25 Feb 1969, *Mavi 983* (NU). Novton, 07 Feb 1932, *Filt 8050* (MO). **S.W.A. (Southwest Africa?):** 8 km S of Makuri vlei on road to Gimsa, small pan on side of road, muddy sand, 03 Mar 1985, *Hines 361* (PRE). **SENEGAL: Kaolak Region:** Kaolak, Nov 1824, *Berhaut s.n.* (Z). **SIERRA LEONE:** *Elliot 4453* (GH). **SOUTH AFRICA: Mpumalanga Province:** Transvaal, Witklip Staatsbos, Nelspruit Dist., in water in Witklipdam, Kruid, 27 Jan 1976, *Kluge 862* (PRE). **Province of KwaZulu-Natal:** Tembe Elephant Park, seasonal pan, locally common, 27^{o} 01S, 32^{o} 29E, 13 Mar 1991, *Ward 2762* (NH photo), North coast, Lake Nhlabane area, western corner of North Lake, 28^{o}36'S; 32^{o}15'E, 19 Sep 1991, *Ward 11378* (PRE, NU, NH photo), Maputaland, Sileza forest reserve, eastern boundary, 22 Feb 1993, *Matthews 1188* (NU, NH photo), Hlabisa, St. Lucia estuary, game park E of Vidal Road, 09 Nov 1977, *Pooley 1942* (NU). **SUDAN:** Jonglei, Nyany, nr. Maar, 80 km N of Bor, 01 Feb 1981, *Lock 81/10* (K). **SWAZILAND:** Malolotja Nature Reserve, below Mortimers dam, stream, 17 Dec 1985, *Heath 406* (PRE). **TANZANIA: Dar es Salaam Region:,** Mbezi, 2km WNW of Dar es Salaam University (by cattle track to Tanzania packers), 12 Jun

1974, *Wingfield 2752* (MO). **Iringa District:** T7, km 13 Ufinda-Sao Hill Rd., E side of road, 8°08'12"S, 35°24'39"E, 10 Jun 1996, *Faden et al. 96/130* (K, US). **Ruvuma Region:** Ruanda, Urundi, Vallie Uruanda, Oct 1953, *Liben 852* (M). Nkansi, 7 km on Namanyere-Kipili Rd, 03 May 1997, *Bidgood et al. 3651* (C). Tanganyika, rare in bog surrounding Lake Kwela, 10 Mar 1959, *Webster 29* (K). Ost-Afrika, 4 Mar 1882, *Bohm 106* (Z). **ZAIRE: Province de l' Equateur:** Bikoro, 01 Oct 1957, *Thonet 7* (M). **Province du Kasai-Occidental:** swampy margins of small lake, Kabinda, 26b Jul 1934, *Becquaert 62* (GH). **Province du Katanga:** River Kalule, pres de la ferme Rostenne, Elisabethville, 27 Mar 1963, *Symoens 10155* (K). **Province Orientale:** 1940, *Germain 171* (M), Parc nat. de la Garamba, env. De Bagbele, 29 Apr 1950, *Noirfalise 223* (K), Isangi, Entre Yambao et Mongandjo, riv. Limbete, 15 Jan 1957, *Evrard 2093* (Z). **ZAMBIA: Central Province:** Mkushi Dist., David Moffat's farm, Munchiwemba dambo, S13°45', E 29°40', 1400 m, 20 Sep 1993, *Bingham & Nkhoma 9711* (PRE). **Luapula Province:** Lake Bangweulu, southern part, swamps between Ncheta Island and Chibambo Lagoon, 11 Feb 1996, *Renvoize 5585* (K), Chipili, 88 m N of Ft. Roseberry, 27 Jun 1956, *Robinson 1761* (NU). **Northern province:** 8 km N of Kasama, swiftly flowing stream, 22 Jan 1961, *Robinson 4296* (K, MO, NU), Mfuwe, Chipaka Dist, occasional in *Oryza* grassland on waterlogged heavy black clay, 13 Mar 1969, *Astle 5605* (K, NU). **Western province:** about 10 miles NE of Mongu, in stream, 18 Nov 1959, *Drummond & Cookson 6597* (MO), Masenga camp, Lukulu flood plain, Bangweulo mpika, seasonal swamp, 20 Apr 1959, *Vesey-FitzGerald 2497* (NU). **ZIMBABWE: Manicaland:** Mare Dam, Rhodes Inyanga National Park, 06 Jan 1972, *Gibbs Russell 1210* (M, MO [2 sheets], K), Melsetter, Tarka Forest Reserve, 1000 m, Nov 1970, *Goldsmith 32/70* (NU). **Matabeleland North:** Wankie National Park, Ngamo Pans 54 miles SE of main camp, 19°06'S, 27°25'E, 17 Apr 1972, *Russell 1645* (NU). **Salisbury District:** 6 mile spruit, 4800', 10 Jan 1932, *Brain 8007* (MO), 4800', 24 Jan 1932, *Brain 8307* (MO, PRE), Hartley, 06 Apr 1952, *Hornley 36229* (MO), Hartley, Avondale Farm dam, wet edges of dam, 25 Feb 1969, *Mavi 983* (K). Bounaensis, 20 km E of Gawi, in pool in savanna, 15 Sep 1967, *Geerling & Bokdam 877* (MO). French Equatorial Africa, Jan 1952, *Koechlin 1628* (NY).

ASIA. CHINA: Huebi: Central China, 1885-1888, *Henry 4102* (GH, US [2 sheets]). **Yunnan:** Open field, 1530 m, May 1936, *Wang 73552* (GH), swampy land near stream, 760 m, Oct 1936, *Wang 80400* (GH). Katsura, 04 Jul 1909, *Sakuraj 51* (GH). Wah Shan Kuek, N.T., Hong Kong, 04 Dec 1970, *Hu 10884* (GH). **INDIA: Bangladesh:** East Bengal, 1863-64, *Griffith 6235* (NY). **Karnataka:** Hassan District, 18 Jun 1970, *Nicolson et al. 228* (MO, US [3 sheets]), near Station, 10 Nov 1971, *Hooper & Gandhi 2373* (MO, NY), Mysore, Mokali on road to Konnanur, 11 Nov 1971, *Hooper & Gandhi 2418* (MO), Mysore, Nagpuri, 02 Jul 1969, *Saldanha 13933* (K). **Kerala:** Malappuram District, flooded and brack lying rice field between Tirurangadi and Parappanangadi, almost sea level, 12 Nov 1993, *Cook & Camenisch 5169* (Z). **Maharashtra:** Pashan, near Poona, lake margin, 30 Dec 1971, *Hooper 112* (K), Nagpur, Limoed, 04 Dec 1965, *Donde 52* (NY). **Nepaul:** without date, *Hook & Thomson s.n.* (NY). **Tamil Nadu:** Dharmapuri, Denkanikotta taluk to Jowalagiri, to Karareddy pond, 18 Dec 1978, *Matthew & Venugopal 20415* (GH). 1831, *unknown s.n.* (BM), Heyneanum, 1831, *unknown s.n.* (BM), Napalia, 1831, *unknown s.n.* (BM [2 sheets]). Assaeu, without date, *Griffiths 1589* (BM), *Griffiths 1600* (BM). Peninsula Ind. Orientalis, 1902, *unknown 1902* (NY), *unknown 3154* (NY), 1831, *Wallich 3453* (NY, P). Loha-Behav, 700', Barra pahov Sambalpern Dissa, 23 Sep 1949, *Mooney 3622* (GH). Ranchi, 22 Oct 1873, *Clarke 20346* (BM). Borhatta, 13 Oct 1885, *Clarke 40768* (BM). *Clarke s.n.* (US), *Hb. Shuttleworth s.n.* (BM). Mountains of Khasia, *Hook & Thomson s.n.* (GH, NY, P). Ind. Orientalis, *Hook & Thomson s.n.* (NY). Mont. Khasia, Regio Prop., Ind. Or., *Hooker & Thomson s.n.* (BM). *Wight? s.n.* (BM). 1862-3, (US). **INDONESIA: Alor:** 1938, *Jaag? s.n.* (ZT). **Java:** Meester Cornelis, 1991, *unknown 23139* (K), Blume, without date, *Zippeluis s.n.* (NY). **Jawa:** Barat, Banten, 1936, *Hackenberg 1* (GH). **JAPAN: Hondo:** Shinjo in Kii, 11 Oct 1953, *Koyama 838* (GH). **Honshu:** Shinjo mura, Nagaitani valley, large colony in shallow water near the edge of a large pool, local pure vegetation, 15 Oct 1953, *Koyama 5885* (MO, NY). **Kyushu-chiho:** Hondo, Shinjo in Kii, 11 Oct 1953, *Koyama 838* (BRIT, NY, US, WIS). **Yoron-jima:** Liukiuensis, 30 Aug 1921, *Uyehara s.n.* (US). Kadsusa, Itinomiya, 16 Jul 1910, *unknown s.n.*(US). **MALAY PENINSULA:** Langkowi, ricefields near Kueh, 14 Nov 1941, *Comes? 37973* (K). **MALAYSIA: Malacca:** Kampong Bukit Piatu, paddy fields, 02 Apr 1955, *Sinclair 40551* (K). **PHILIPPINE ISLANDS: Lanao Mindanao:** in 6" of water pocket in grassland , 04 Sep 1938, *Zwickey 50* (GH, US). **Lano Province: Mindanao:** Mountains, Mamaguintang and Camangan , 26 Feb-30 Mar 1941, *Ebalo 1047* (GH). Caloocan, Prov. Rizal, Luzon, Oct 1909, *Merrill 520* (Z). Camp Keithley, Lake Lanas, Mindanar, June 1907, *Clemens 1115* (F). Manila and vicinity, Dec 1914, *Merrill 9790* (NY). Vicinity of Tanculan, Bukidon subprovince, Mindanao, Jul 1916, *Fenix s.n.* (K, NY, US). **SIAM:** Growing in open fields, 13 Jul 1968, *Kerr 15798* (K). **SRI LANKA: North Eastern Province:** Amparai District, Helawe Eliya, ca. 7 miles S of Panama, E of Helawe Lagoon, sea level, 08 Feb 1971, *Koyama et al. 14026* (GH, NY), Anuradhapura District, between Tirappana and Galkulama, periodically flooded big swamp, 09 May 1968, *Koyama 13591* (GH, NY, US). 1870, *Thwaites 3162* (BM, GH, P [2 sheets]). **VIETNAM: Quang Nam-Dà Nang: Tinh (province):** Annam, Mount Bani; in the main coast range about 25 km from Tourane (Da Nang), May-July 1927, *Clemens & Clemens 4050* (F, K, MO, NY, PH, US, US, Z). Cochinchine, 1862-1866, *Thorel 464* (P). Dalat Lac Xuan huong, 22 Aug 1967, *Vu-Van-Cuong 521* (P). Cochinchine, without date, *Pierre s.n.* (P).

OCEANIA. AUSTRALIA: Queensland: Cook District, Abattoir swamp, 4.5 km N of Mount Molloy, 20 May 1995, *Clarkson 10317* (BRI), Cairns, in water in wet forest country, 15 Jun 1935, *Blake 9371* (K, NY [2 sheets]), Brisbau River, Dec 1891, *Von Mueller s.n.* (M). **PAPUA-NEW GUINEA: Morobe District:** vicinity of Kajabit Mission, elev. 800-2000 ft., Aug-Dec 1939, *Clemens 10600* (GH, US). **National Capitol District:** Hohola Port Moresby, in clumps in small seasonal lagoon in *Eucalyptus* savannah, 14 Nov 1973, *White 37815* (BRI, GH, K, M, US). Dagwa, Oriomo River, Fer-Mar 1934, *Brass 6010* (BRI, NY).

APPENDIX V

ELEOCHARIS ACUTANGULA SUBSP. *BREVISETA* SPECIMENS EXAMINED

(PARATYPES)

NORTH AMERICA. U.S.A: Florida: Lee Co.: Wild Turkey Strand Natural Area, about 2.5 air miles SW of the intersection of Hwy. 82 and Green Meadows Rd., SE of Fort Myers, N26° 32' 17.3" W81° 42' 12.9", 12 Nov 2004, *Rosen & Carter 3206* (CIIDIR, GH, K, MICH, MO, TAES, TEX, US, VSC, WIS), S side of Griffin Rd., just S of entrance to Pinewood Lakes in Gateway, ca. 0.5 mi E of jct Gateway Blvd, ca. 9 mi SE of downtown Fort Myers; Alva SW 7.5' Quad, SWQ, SWQ, Sec. 8, T45S, R26E, 26° 34'12"N, 81° 44'27"W, 28 Oct 1993 *Orzell and Bridges 22526* (BRIT, FTG, USF). **MEXICO: Estado de Campeche:** zona inundable a los alrederores de China, a aprox. 10 km al sureste de la ciudad de Campeche. Mun. Campeche. Alt. 80 m. Creciendo en al area inundada, en las partes mas de 70 cm, 10 Nov 1980, *Novelo & Zetina 721* (TEX), grassy ridge with ponds 14 km N of Ocozocoautla on road to Mal Paso, Municipio of Ocozocoautla de Espinosa, 07 Oct 1974, *Breedlove 38254* (MEXU, MO). **Estado de Chiapas:** wooded slopes along stream, 96 km S of Mexican Hwy. 190 on road to Nuevo Concordia, 10 Oct 1974, *Breedlove 38516* (NY). **Estado de Guerrero :** 1.5 km al NW del Rincon de la Via, 17°17'55", 99°29'28", bosque de pino-encino, 28 Sep 1988 *Verduzco 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 Tecumen Province, muddy swamp, common, 11 Dec 1923, *Standley 26509* (MO). **Canal Zone:** Laguna de Portala, near Chepo, province of Panama, Oct 1911, *Pittier 4602* (NY). **Provincia de Panama:** Sabanas near Chepo, 30 m, 20 Jan 1935, *Hunter & Allen 87* (MO), muddy bog, one mile 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 28909* (US), near Matias Hernandez, wet field, 30 Dec 1923, *Standley 28984* (US).

CARIBEAN BASIN. CUBA: Provincia de Ciudad de La Habana : Vedado-Habana, Sabana de Monasterio, 23 Jun 1920, *Leon 9215* (NY). Without location, 1860-1864, *Wright 3376* (GH, mixed with E. mutata, MO, NY, P). **DOMINICAN REPUBLIC: El Seibo Province:** roadside ditch near Seibo, vicinity of Higuey, 3-7 Nov 1946, *Howard & Howard 9862* (GH, NY [2 sheets], P, US).

SOUTH AMERICA. COLOMBIA: Departamento del Magdalena,: savana, Rincon Hondo, Magdalena Valley, growing in water, 10 Aug 1924, *Allen 357* (MO). **Departamento del Vaupes :** Rio Vaupes, Mitu y alrededores, 08 Sep 1951, *Schultes & Cabrera 13977* (GH), Rio Vaupes, Mitu and vicinity, 1°0'N, 70°5'W, 09 May 1953, *Schultes & Cabrera 19257* (GH [2 sheets]). **VENEZUELA: Estado Bolivar:** 27 km SW of Caicara along Hwy. 19 to Ciudad Bolivar, 22 Nov 1973, *Davidse 4355* (MO). **Estado Tachira:** level area in valley, open pastures and fields with natural swampy depressions, between La Rochela and La Espuma, SW of Santo Domingo, 31 Jul 1979, *Steyermark & Liesner 119299* (MO). **Estado Zulia:** Perija, carretera Calle Larga-San Felipe-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). **GUYANA: Upper Takutu-Upper Essequibo Region:** Rupununi savannas, Baboon Hill (Sabrina Tau) 1.5 km S of Sand Creek Village, 21 Jun 1989, *Gillespie et al. 1803* (NY). **ECUADOR: Provincia de Los Rios:** along road San Juan, Vince, 07 Mar 1988, *Laegaard & Renvoize 70652* (K, NY). **BRAZIL: Estado de Mato Grosso do Sul:** Pantanal do Miranda-Abobral, Passo do Lontra, Rodovia MS 122, Fazenda Sao Bento, depois da 2a porteira, 19° 28' 32"S, 57°02'39"W, 11 Jul 1997, *Rodrigues et al. 3* (K). **Estado de Rondonia:** Guapore, Porto Velho, 1952, Cordeiro & Silva *270* (US). **Estado do Amapa:** Rio Macacoari, Municipio de Macapa, 05 Aug 1951, *Froes & Black 27231* (US). **Estado do Parana:** Curitiba, Paso do Lontra (mun. Miranda) Mato Grosso, 13 Oct 1972, *Hatschbach & Scherer 30441* (NY, Z). **Estado do**

Rio de Janeiro: Rio de Janeiro, Jan 1914, *Hoehne 5736* (US). **Estado do Rio Grande do Sul,** Jari, estrada do Caracuru, Jari, estrada do Caracuru, campo alagado, 09 Aug 1969, *Silva 2636* (NY). **Estado do Roraima,** borrow pit close to road from Furo do Maraca to SEMA research station, 10 Mar 1987, *Edwards 2529* (K). **BOLIVIA: Departamento del 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. GHANA: Northern: Gambaga road, 2 miles from Walewale, 07 Dec 1950, *Adams 4201* (NY; probably *Eleocharis* aff. *acutangula* subsp. *breviseta*). **SOUTH AFRICA: Province of KwaZulu-Natal:** Hlabisa, St. Lucia, eastern shores, 30 Nov 1959, *Feely & Ward 15* (K, M, NU [2-sheets]), Near Howick, in flooded dam, 1990, *Taylor 131* (NU), Ingivauvima distr., near Salumhlanga, Ndumu Game Reserve, 22 Dec 1972, *Pooley 1624* (NU), Greater Durban area, Mlazi Valley, 29°54's; 30°49'E, 15 Mar 1992, *Ward 11925* (NU, PRE), Greater Durban area, Mlazi Valley, 29°54's; 30°48'E, 15 Mar 1992, *Ward 11926* (NU, NH photo), Transvaal, Waterberg, 13.2 m NW of Warmbaths, 19 Mar 1965, *Acocks 23562* (K, PRE), near Maputa, Tengane near Nyinyani dip tank, 29 Oct 1980, *Cunningham s.n.* (NU), Karkloof floodplain near junction with Kusane River, Jan 1977, *Kotze s.n.* (NU). **TANZANIA: Singida Dist.:** T. 5, M. 12.7 from Issuna on the Singida-Manyoni Road, 4,800 ft., 13 Mar 1964, *Greenway & Polhill 11,543* (PRE), T4, Sumbawanga District, goli Mbuga, 5 km S of Sumbawanga, 7°59'52"S, 31°3'55"E, 19 Jun 1996, *Faden et al. 96/302* (US), T5, Manyoni District, Chaya Lake, S of Itigi-Tabora track, 16 km W of Kazikazi, 5°34'57"S, 34°03'54"E, 02 Jul 1996, *Faden et al. 96/522* (US). **ZIMBABWE:** Gokwe, Sengwa Nature Resreve, 18°2'S, 28°50'E, Jan 1966, *Jacobsen 73* (NU), District Gokwe, Sengwa research station, 09 May 1966, *Jacobsen 3218* (PRE).

APPENDIX VI

ELEOCHARIS OBTUSETRIGONA SPECIMENS EXAMINED

NORTH AMERICA. U.S.A: Texas: Cameron Co.: in water four miles E of Rio Hondo, 08 Feb 1934, *Clover 1752* (MICH, TEX); 20 miles N of Brownsville, bordering the Paredes Rd., form large colonies, wet ground and deep wet ditches, 16 Jun 1941, *Runyon 2765* (TEX); Laguna Atascosa National Wildlife Refuge, ca. .9 mi. S of entrance to Unit 1, near main road, in ca. 20-40 cm water, dark brown clayey sand, *Sagittaria* sp., *Solanum* sp. *Acacia berland*. complex, in clonal masses, 23 Jul 1959, *Traverse 1060* (BRIT, TEX). Kennedy Co.: south of Armstrong, near highway 96, 17 Oct 1938, *Runyon 1953* (TEX; cited by González-Elizondo et al. 2002, but not seen by author). **MEXICO: Estado de Veracruz-Llave:** Rancho de la Secretaria de Salubridad y Asistencia (Antes Rancho 3 Pasos), Emilano Zapata, 19^{o} 32 N, 96^{o} 50W, encinar perturbado, secundaria, suelo en una characa, aquatica, 15 Apr 1977, *Ortego 673* (F, MEXU); Mpio. Xalapa, Military camp aside Fracc. Tres Pasos, ca 9 km ESE of the city of Xalapa, along rural road N of Hwy. 140 that terminates at Military Camp, 14 Jul 2006, *Rosen et al. 3875* (CIIDIR, GH, K, MICH, MO, TAES, TEX, US, VSC, WIS); Miradores, municipio de Dos Rios, dentro del agua de la presa, 14 Oct 1974, *Ventura 10639* (WIS).

CENTRAL AMERICA. EL SALVADOR: shallow water, mud bottom, Laguna Verde, Apaneca, 30 Dec 1950, *Fassett 28528* (F). **GUATAMELA: Dept. Jutiapa:** Lago Retana, between Ovejero and Progresso, 600 m, 26 Nov 1939, *Steyermark 32006* (F). **HONDURAS: Comayagua:** in marsh near Siguatepeque, 1050 m, 9 Jul 1936, *Yuncker et al. 5760* (F, GH, MO; mixed with *E. acutangula*, NY; mixed with E. acutangula). **Morazan:** vicinity Agua Amarilla and Hoya Grande, 27 Oct 1989, *Molina 34176* (MEXU). **NICARAGUA: Dept. Esteli:** along carretera Norte, 11 km N of Esteli, 13 Aug 1978, *Vincelli 858* (CIDDIR, MEXU, MO). **COSTA RICA: Cartago:** Laguna Concavas, Canton Paaiso, 22 Aug 1983, *Lot & Novello 1214* (MEXU).

SOUTH AMERICA. ECUADOR: Galapagos Archipelago: Chatham Island, Wreck Bay, common in pools of water, 23 Feb 1905-1906, *Stewart 1080* (MO, NY); Indefatigable Island, in cut *Miconia* behind Schiess farm, to 1 m, growing in 20 cm deep water, 25 Jul 1974, *van der Werff 1313* (MO); San Cristobal Island, 22 Sep 1932, *Schimpff 119* (M, MO, NY, P, US, Z [2 sheets], US). **BRAZIL: Bahia:** ca 0.5 km SW of Jussiape by the Rio de Contas, on the road to Marcolino Moura, riverside marsh, 26 Mar 1977, *Harley 20029* (E, NY); municipio de Belmonte, km 60 a 68 da Rodovia Itapebi/Belmonte, 09 Jun 1980, *Silva & Brito 942* (NY). **Minas Gerais:** 21 km N of Medina along Hwy. BR-116, marsh with open water in center and grassy margin, 670 m, 30 Mar 1976, *Davidse et al. 11585* (MO, NY); Municipio Lagoa Santa, 19^{o}40'S, 43^{o}55'W, 835 m, 03 May 1952, *Smith 6710* (GH, NY, P, US); Lagoa Santa, 28 Nov 1863, *Warming s.n.* (C [3 sheets]). **Rio de Janeiro:** 1816-1821, *Catal s.n.* (P); Rio Grande do Sul, Munic. De Triunfo, lugar brejoso, 22 Jan 1964, *Pereira & Pabst 8527* (M); Rio Grande do Sul, in paludosis, Mar 1935, *Rambo 1045* (MO); Dec 1892, *Weruor? 548* (ZT); Rio de Janeiro, Monerat, Feb 1952, *Capell 9* (US). **Sao Paulo:** capital, parque da agua branca, 02 Jun 1948, *Joly 16895* (NY). Sao Christovao, dams les fosses, 19 Nov 1872, *Glaziou 6422,* (P [2 sheets]). SE Brasilia, without date, *unknown* (C). **PARAGUAY: Dept. Central:** Estero del Ypoa, 10 km SW of Nueva Italia, S of Canada, floating island, 25^{o}20'S, 57^{o}28'W, 27 Jan 1990, *Zardini & Velazquez 18483* (MO). **Dept. Misiones,** La Soledad, Santiago, shallow water, 23 Dec 1965, *Pedersen 7634* (C, GH, K, NY, P, US). **Dept. Neembucu,** Dist. Yataity, Frutos Atras, emergent from shallow water center of marsh, Feb 1975, *Walter 138* (PH). 1885-1895, *Hassler 1415* (P, NY). **ARGENTINA: Corrientes Prov.,** General Paz, 6 km SW de Caa-Cati. Ruta 13, en cultivo de arroz, 16 Mar 1978, *Ahumada 1966* (MO); Concepcion, Tabay, Orilla de laguna, palustr, 29 Mar 1975, *Arbo et al. 977* (NY); La Yela, Empedrado, in stagnant water one foot or more deep, with muddy bottom, 12 Mar 1987, *Pedersen 14845* (C); Carambola, Concepcion, foot-deep water, among the reeds, 24 Apr 1982, *Pedersen 13389* (C, GH, NY); San Cosme, shallow lake, growing with other swamp weeds in about 6 ins. of water, 26 Nov 1961, *Pedersen 6399* (C, GH, P); Santa Teresa, Mburucuya, 21 Jan 1951, *Pedersen 957* (GH, NY, US). **Entre Rios Prov.,** Buena Esperanza, Federacion, shallow muddy waterhole, 03 Feb 1967, *Pedersen 8055* (C, K, NY). **Formosa Prov.,** Pilcomayo, Parque Nac. Pilcomayo, banados del borde de la Laguna Blanca, 13 Dec 1988, *Guaglianone & Mulgura 2196* (NY). **Salta Prov.,** Candelaria, aqua caliente, 1000 m, Feb 1925, *Venturi 3667* (GH). **Tucuman Prov.,** Rio Chico, Los Saruieato (sic), 500 m, 10 May 1929, *Venturi 8485* (GH [2 sheets]; MO); Mouteros, 450 m, 20 Nov 1921, *Venturi 1438* (US).

VITA

Name: David Jonathan Rosen

Address: S. M. Tracy Herbarium
Department of Rangeland Ecology & Management
Texas A&M University
College Station, TX 77843-2126

Education: B.S. (*summa cum laude*), Biology, Texas State University, 1996
M.S., Rangeland Ecology and Management, Texas A&M University, 1998
Ph.D., Rangeland Ecology and Management, Texas A&M University, 2006

Select Publications:

Rosen, D. J. 2006. New and disjunct records of *Eleocharis liesneri* (Cyperaceae) from South America. Sida 22:781-786.

Rosen, D. J., R. Carter, and C. T. Bryson. 2006. The recent spread of *Cyperus entrerianus* (Cyperaceae) in the southeastern United States and its invasive potential in bottomland hardwood forests. The Southeastern Naturalist 5: 333-344.

Rosen, D. J. and S. L. Hatch. 2006. New records of *Eleocharis obtusetrigona* (Cyperaceae) from Central and South America. Brittonia 58: (in press).

Rosen, D. J. and W. L. Miller. 2005. The vascular flora of an old-growth Columbia Bottomland forest remnant, Brazoria County, Texas. Texas Journal of Science 57:223-250.

Rosen, D. J. and R. B. Faden. 2005. *Gibasis pellucida* (Commelinaaceae), a new and potentially weedy genus and species for Texas. Sida 21:1931-1934.

Rosen, D. J. and S. D. Jones. 2004. *Eleocharis mutata* (Cyperaceae) new to the flora of North America north of México. Sida 21:1153-1160.

Rosen, D. J. and B. J. Christoffersen. 2004. Rediscovery of *Cyperus cephalanthus* (Cyperaceae) in Texas. Phytologia 86:107-109.

Rosen, D. J. 2004. Noteworthy collections of *Cyperus drummondii* (Cyperaceae) from Texas. Sida 21:495-497.