

Eastern Illinois University

From the Selected Works of Gordon C. Tucker

1984

Taxonomic notes on two common neotropical species of *Cyperus* (Cyperaceae)

Gordon C. Tucker, *Eastern Illinois University*

TAXONOMIC NOTES ON TWO COMMON NEOTROPICAL SPECIES OF CYPERUS (CYPERACEAE)

GORDON C. TUCKER

Department of Botany, Duke University
Durham, NC 27706, U.S.A.

ABSTRACT

The results of a herbarium study of two common species of *Cyperus* (*C. manimae* and *C. odoratus*) are presented. It is shown that: 1) in *C. manimae*, the varieties *asperimus*, *divergens* and *phaeocephalus* do not merit recognition; 2) *C. spectabilis* Link and *C. apiculatus* Liebm. should be treated as synonyms of *C. manimae*; and 3) *C. macrocephalus* Liebm., *C. eggersii* Boeck., *C. acicularis* (Schrad.) Steud. and *C. engelmannii* Steud., are synonyms of *C. odoratus* L.

INTRODUCTION

In the course of an investigation of the Mexican and Central American species of *Cyperus*, the taxonomic status of two species, *C. manimae* and *C. odoratus*, has been altered. Since these are two of the commonest species of the region, it seems desirable to publish these findings in advance of completion of the study. The present study has been based on some 13,000 herbarium specimens from 33 herbaria. About 90% of these specimens were collected in Mexico and Central America, the remainder in North America, South America and the Old World.

I. The status of *C. manimae*, *C. spectabilis* and *C. apiculatus* (Subgenus *Cyperus*).

Cyperus manimae is one of the most common species of *Cyperus* in the mountains of Mexico, particularly in the pine and oak forests from about 2000–2700 m elevation. The species ranges from the southwestern United States through Central America to Venezuela and Peru. Both Kükenthal (1935–36) and Ayers (1946) also recognized *C. spectabilis*, which was distinguished only by its lax spikes usually borne on rays; typical *C. manimae* was described as having dense spikes and often lacking rays. According to Kükenthal the range of *C. spectabilis* was nearly the same as that of *C. manimae*.

In the present study, numerous specimens with sessile spikes were observed, as well as collections in which the rays were as much as 16 cm long (see Fig. 1). The length of the rays was not significantly correlated with the height of the culm. Thus, *C. spectabilis* could not be distinguished

based on sessile versus pedunculate spikes. Several other species, e.g. *C. luzulae* (L.) Retz. (Denton, 1978) and *C. haspan* L. (Tucker, 1983) similarly have both sessile and pedunculate forms.

The second problem in distinguishing *C. spectabilis* and *C. manimae* lay in the lack of a clearcut difference between dense and lax spikes. About one-quarter of the collections examined was clearly intermediate with respect to the density of the spikelets on the rachis of the spikes. Some 100 typical examples of *C. manimae* and *C. spectabilis* were studied critically with the hope of finding other characters that might be correlated with the density of the spikes. Achene length and width, scale length, width and color, mucro length, culm roughness and ray length were investigated. None showed positive correlation with the density of the spikes. Thus, it is concluded that the populations previously classified as *C. spectabilis* merely represent a portion of the range of variability of *C. manimae* in one character. Thus, *C. spectabilis* is here considered to be a synonym of *C. manimae*.

Both Kükenthal (1935-36) and Ayers (1946) recognized the Mexican species *C. apiculatus* Liebm. Ayers distinguished *C. apiculatus* from *C. manimae* by the former species having: fewer inflorescence bracts, wider scales, and longer, iridescent achenes. He cited ten collections of *C. apiculatus*, eight of which were seen in the present study: Mexico. Distrito Federal: *Bourgeau* 432 (GH); Guerrero: Manchón, *Hinton* 9244 (K, LL, MICH); Jalisco: Guadalajara, *Pringle* 3844 (K, LL, MSC); Huejoritán, *Diguet s.n.*, Oct. 1912 (K); Michoacán: vic. Morelia, *Arrène* 2692a (GH), 5579 (NY), 5751 (MO), and 5844 (GH, MO). On the basis of these collections, it could not be shown that *C. apiculatus* differed from *C. manimae* in any of the characters listed by Ayers. For the above specimens, the average number of inflorescence bracts per plant was 3; the average for *C. manimae* (based on examination of some 400 collections from throughout its range) was 4. For scales, the average measurements were 2.2 mm long and 1.6 mm wide for *C. apiculatus*, versus 2.1 mm long and 1.8 mm wide for *C. manimae*; and for achenes 1.5 mm long and 0.8 mm wide, versus 1.6 mm long and 0.8 mm wide.

Several collections cited by Ayers (for example, *Pringle* 3844) had glossy achenes. Ayers used the word "iridescent", which is inappropriate. Kükenthal (1935-36) used the term "nitida" to describe the achenes of both *C. manimae* and *C. apiculatus*. This is accurate, although both dull and glossy achenes were observed in *C. manimae*.

To summarize, the present author found no evidence to support the recognition of *C. apiculatus*. None of the differences used by Ayers could be confirmed when a sufficiently large sample of *C. manimae* was examined, nor could any other consistent differences be detected. Thus, *C. apiculatus* is synonymized with *C. manimae* in this treatment.

Kükenthal recognized four varieties in both *C. manimae* and *C. spectabilis*. Ayers did not recognize any of Kükenthal's varieties of *C. spectabilis*. He

did recognize those in *C. manimae*, stating that there was "bewildering" intergradation between the varieties of *C. manimae*, particularly between the red and brown scaled varieties. Typical *C. manimae* has smooth culms, and blunt, brown scales. According to Ayers, the varieties are distinguished as follows: var. *asperimus*, culms rough; var. *divergens*, scales mucronate; and var. *phaeocephalus*, scales red (see table I).

None of these varieties possessing supposedly distinguishing features has a distinct range—all occur more or less throughout the range of the species. In addition, some plants are found to exhibit the distinguishing features of more than one variety. For example, *Sharp and Gilly 156* (MSC) from Distrito Federal, and *Standley 61276* and *61277* (F), from Escuintla, Guatemala, both have rough culms and red scales. Similarly, *Pennell 18869* (GH, PH) from Chihuahua, Mexico, and *Williams et al. 22163* (F, NY) from

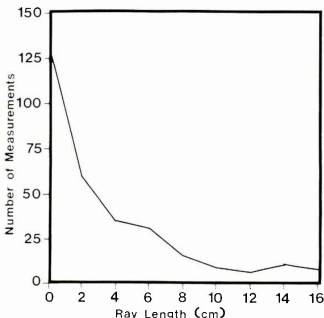


Fig. 1. Frequency distribution of ray lengths in *Cyperus manimae*, including those plants treated by Kükenthal (1935-36) and Ayers (1946) as *C. spectabilis*.

Huehuetenango, Guatemala have scales that are red and mucronate.

Ayers did not state the mucro length of the scales of *C. minimae* var. *divergens*. From examination of cited specimens, he apparently had in mind plants with mucros longer than 0.3 mm. The length of mucros in collections studied show a continuous distribution from less than 0.1 mm to about 0.7 mm (see Fig. II.) Thus, a division between blunt and mucronate varieties would be arbitrary. Similar intergradation between red and brown scaled forms was observed. The most distinctive of the named varieties of *C.*

Table I. Comparison of the distinguishing features of the four varieties of *C. minimae* H.B.K. as recognized by Ayers (1946).

VARIETY	CULMS	SCALE APEX	SCALE COLOR
<i>minimae</i>	smooth	blunt	brown
<i>asperius</i>	hirsellate or scabrous	blunt	brown
<i>divergens</i>	smooth	conspicuously mucronate	brown
<i>phaeocephalus</i>	smooth	blunt	deep red

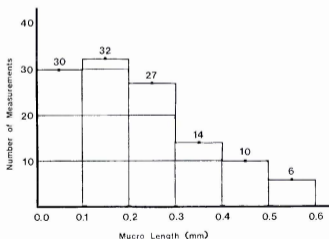


Fig. II. Frequency distribution of mucro lengths in *Cyperus minimae*.

manimae was var. *asperrimus*. Nearly all plants of *C. manimae* have either culms that are densely scabrous in the upper half (var. *asperrimus*) or entirely smooth (remaining varieties). However, in several collections, the culms were rough only in the uppermost 1–2 cm, thus providing an intermediate state between var. *asperrimus* and the typical variety.

To summarize, each of these three characters (culm surface, scale apex, and scale color) used by Ayers and by Kükenthal to distinguish the three varieties of *C. manimae*, exhibits considerable intergradation between the condition ascribed to typical *C. manimae* and that of the particular named variety. None of these character states has a discrete geographic range. Thus, it is appropriate to treat these three varieties as synonyms of *C. manimae*. The synonymy of *C. manimae* is given below.

CYPERUS MANIMAE H.B.K.

- C. manimae* Kunth in H.B.K., Nov. gen. sp. 1:209. 1816. TYPE: VENEZUELA. Orinoco River at Atabapo, *Humboldt & Bonpland* (HOLOTYPE: P). *Mariscus manimae* (H.B.K.) C. B. Clarke, Contr. U. S. Natl. Herb. 10:452. 1908.
- C. divergens* Kunth in H.B.K., Nov. gen. sp. 1:208. 1816. TYPE: MEXICO. Jorullo, *Humboldt & Bonpland* (HOLOTYPE: P). *C. manimae* var. *divergens* (H.B.K.) Kükenth., Pflanzenreich 4(20):463. 1936.
- *C. spectabilis* Link, Hort. Berol. 1:318. 1827. TYPE: not located.
- *C. triceps* Nees, Linnæa 19:697. 1847. TYPE: MEXICO. *Aschenborn* 121 (HOLOTYPE: not located; ISOTYPE: B!).
- *C. scaberrimus* Nees, Linnæa 19:697. 1847. TYPE: MEXICO. *Aschenborn* 123 (HOLOTYPE: not located; ISOTYPE: B!). *C. spectabilis* var. *scaberrimus* (Nees) Boeck, Linnæa 35:606. 1868.
- C. apiculatus* Liebm., Mexic. halvgr. 32. 1850. TYPE: MEXICO. Puebla, San Antonio Huatusco, Aug 1841, *Liebm. 14352* (HOLOTYPE: C!).
- C. asperimus* Liebm., Mexic. halvgr. 30. 1850. TYPE: MEXICO. Consoquieta, Aug 1841, *Liebm. 14416* (HOLOTYPE: C!; ISOTYPE: HAL!). *C. manimae* var. *asperimus* (Liebm.) Kükenth., Pflanzenreich 4(20):463. 1936.
- C. asperimus* var. *multiflorus* Liebm., Mexic. halvgr. 31. 1850. TYPE: MEXICO. Mirador, *Liebm. 14415* (HOLOTYPE: C!; ISOTYPE: K!).
- C. spectabilis* var. *multiflorus* Boeck, Linnæa 35:607. 1868. TYPE: MEXICO. *Schmitz* 808 (not located).
- C. phaeocephalus* Griseb., Abh. Goett. Ges. Wiss. 19:216. 1874. TYPE: not located. *Mariscus phaeocephalus* (Griseb.) C. B. Clarke, Kew Bull. Addit. Ser. 8:16. 1908. *C. manimae* var. *phaeocephalus* (Griseb.) O'Neill & Benedict, Leaf. W. Bot. 4:36. 1944.
- C. buckleyi* Britton, Bull. Torrey Bot. Club 13:207. 1886. TYPE: U. S. A. Texas, *Buckley s.n.* (LECTOTYPE: NY!; ISOLECTOTYPE: GH!). [Britton cited three collections, but did not specify a type. Buckley's collection has been annotated "type" in Britton's hand. Thus it is the lectotype.]
- C. parryi* Britton ex C. B. Clarke, Kew Bull. Addit. Ser. 8:9. 1908. TYPE: MEXICO. San Luis Potosí, *Parry & Palmer* 906 (LECTOTYPE, here designated: NY!; ISOLECTOTYPES: GIE US!). *C. spectabilis* var. *parryi* (C. B. Clarke) Kükenth., Pflanzenreich 4(20):462. 1936.
- C. manimae* var. *pseudospectabilis* Kükenth., Pflanzenreich 4(20):463. 1936. TYPE: MEXICO. Puebla, Chinantla, *Liebm. 14460* (LECTOTYPE, here designated: C!).

II. *Cyperus odoratus* and segregate species (Subgenus *Torulinium* (Desv.) Kükenth.)

This pantropical and warm temperate species is exceedingly variable. Numerous segregates have been named. Various authors have treated these as species, varieties or synonyms of *C. odoratus*. These varied opinions were probably the result of a small number of collections seen by any one worker. In the present study, some 800 sheets of *C. odoratus* were examined, from Mexico and Central America, as well as a smaller number from North America, the West Indies and South America.

O'Neill (1940) in his treatment of the sedges of the Yucatan Peninsula recognized five species in Subgenus *Torulinium*. Ayers (1946) followed O'Neill's taxonomic concepts in his treatment of the genus in Mexico. O'Neill distinguished these five species as follows.

- Achene linear, 1.5–2.0 mm long, 0.3 mm wide; scales usually distant, the apex of one not reaching the base of the next on the same side of the rachilla; wings of the rachilla linear, 1.2 mm long, 0.2 mm wide, reaching to top of the achene.
- Leaves and bracts membranous, 1–4 (rarely 6) mm wide; culms 1–2 mm thick at the base *C. engelmannii* Steud.
- Leaves and bracts coriaceous, 8–16 mm wide; culms 5–10 mm thick at the base *C. acicularis* (Nees) Steud.
- Achene oblong to obovoid; scales imbricated on the same side of the rachilla; wings of rachilla elliptic, frequently not extending beyond the middle of the achene, 1.0 mm long, 0.4–0.5 mm wide.
- Inflorescence congested into a single globose compact head 2–3 cm in diameter; the spikes sessile; achene ellipsoid; culms sharply triquetrous; leaves 4–6 mm wide *C. macrocephalus* Liebm.
- Inflorescence with some rays; some of the spikes pendulous; achenes obovoid-oblong to linear-oblong.
- Spikelets suberect, penicillate, very densely fascicled at the ends of the rays *C. eggersii* Boeck.
- Spikelets divaricate, subdense, scattered along the rachis *C. odoratus* L.

Kükenth (1935–36) recognized *C. eggersii* and *C. macrocephalus* as distinct species, while treating *C. acicularis* and *C. engelmannii* as a variety and subspecies, respectively, of *C. odoratus*. Koyama (1978) reduced *C. acicularis* to the synonymy of *C. odoratus*. Correll and Johnston (1970) recognized *C. macrocephalus* as a species, but stated that it intergraded through the "form" *C. eggersii* to *C. odoratus*.

According to O'Neill's key, *C. engelmannii* and *C. acicularis* both have narrower achenes than the other three species. However, in the present study, no plants were observed with achenes less than 0.5 mm wide. Thus, none of the specimens studied would key out to *C. acicularis* or *C. engelmannii*, by O'Neill's criteria. Mature achenes were ellipsoid to oblong, but no linear achenes were noted, thus bringing O'Neill's distinction between these species into question. In the above key, these two species also differ from the others in having scales distant on the rachilla, i.e. the apex of a

scale not reaching the base of the scale above it. It was earlier shown (Tucker, 1983) that in southern Central America, *C. acicularis* could not be distinguished from *C. odoratus* on the basis of the overlap of the scales. The same situation has been noted in the Mexican and northern Central American material of *C. odoratus*.

A comparison of specimens annotated by O'Neill as *C. engelmannii* and *C. odoratus* revealed a continuous range in the amount of overlap or separation of successive scales on the same side of the rachilla. In some plants determined as *C. engelmannii*, successive scales are separated by as much as 0.6–1.0 mm; in others, the separation was less, 0.2–0.6 mm; still other plants are noted in which the scales overlap by approximately 0.2 mm and yet are separated by as great a distance on different spikelets at a comparable state of maturity on the same plant.

Ayers (1946, p. 55) stated that:

"In most of the United States, *C. engelmannii* is a very distinct entity. In Yucatan it is less distinct and in Brazil the line between *C. odoratus* and *C. engelmannii* is still more difficult to draw."

The taxonomy of *C. engelmannii* and *C. odoratus* in the United States has not been investigated in this present regional study. Voss (1972) noted that, in Michigan, *C. engelmannii* suggested an abnormal form of *C. odoratus*. Fernald (1950) recognized *C. odoratus* and *C. engelmannii*, although the number of collections of these species from the U. S. at the Gray Herbarium make it evident that he did not see a large sample. The infraspecific variation of *C. odoratus* in the U. S. is probably much the same as that observed in Mexican collections. The large number of specimens from Mexico and all of Central America examined in the present study, as well as a previous study (Tucker, 1983), has not revealed a single character separating *C. engelmannii* from *C. odoratus*.

Ayers (1946, p. 55) noted that *C. macrocephalus* "... is quite distinct along the Rio Grande, but further south forms intermediate between it and *C. eggersii* occur." Correll and Johnston (1970) stated that *C. macrocephalus* appeared to intergrade through the "form" *C. eggersii* into *C. odoratus*. A critical analysis of specimens annotated by O'Neill, plus numerous more recent collections, revealed the following quantitative characters that differed between these three taxa (see Table II). No further differences could be found between these three taxa, although numerous other characters, particularly those in O'Neill's key, were checked. On the average, *C. eggersii* and *C. macrocephalus* have shorter scales, shorter anthers and shorter achenes than *C. odoratus*. However, there is an overlap in the ranges of each character, and none exhibits a discontinuous distribution between any pair of species. While there is no single difference that consistently separates either *C. eggersii* or *C. macrocephalus* from *C. odoratus*, there is a partial correla-

Table II. Summary of examination of the characters used by O'Neill (1940) to distinguish *C. odoratus*, *C. eggersii* and *C. macrocephalus*. The values given are means and standard deviations. Sample sizes: *C. odoratus*, 255 collections; *C. eggersii*, 44; *C. macrocephalus*, 40. An average of five measurements of each character was made on each specimen.

	C. ODORATUS	C. EGGERSII	C. MACROCEPHALUS
Scale length (mm)	2.4 \pm 0.4	2.0 \pm 0.4	2.1 \pm 0.2
Anther length (mm)	0.5 \pm 0.1	0.3 \pm 0.1	0.25 \pm 0.1
Achene length (mm)	1.4 \pm 0.2	1.2 \pm 0.1	1.2 \pm 0.1

tion of denser inflorescences with shorter scales, anthers and achenes. This might be indicative of some sort of genetic linkage of these characters, or a similar response of these parts of the plants to a certain environmental condition.

The absence of morphological discontinuity between *C. odoratus* and *C. eggersii* and *C. macrocephalus* in the three above characters and the observed intergradation of inflorescence forms among these three taxa, provide evidence that *C. macrocephalus* and *C. eggersii* are conspecific with *C. odoratus*. Several other New World species of Mexican *Cyperus* also have forms with dense rayless inflorescences, e.g. *C. luzulae* and *C. manimae*, an observation noted by Correll and Johnston (1970) as well.

Kükenthal (1935-36) treated *C. bayesii* (C. B. Clarke) Standley as a variety of *C. odoratus*. A previous study (Tucker, 1983) showed this to be a well marked species of the Pacific coast of Central America; *C. bayesii* is closely related to *C. correllii* (Koyama) Tucker⁴ of the Bahama Islands. Thus *C. bayesii* is properly removed from the synonymy of *C. odoratus*.

Kükenthal (1935-36) included *C. purpureo-vaginatus* Boeck. as a synonym of *C. odoratus*. Examination of the type from Warming's herbarium (C), shows that the plant is really *C. distans* L.f. The continuous rachilla, the secondary rays and deciduous scales clearly indicate that it is a member of the subgenus *Cyperus*. Thus, the name *C. purpureo-vaginatus* is properly removed from the synonymy of *C. odoratus*, and belongs with *C. distans*.

The type of *C. odoratus* is Sloane's plate in his work on the natural history of Jamaica (Exell, 1944). This is the only reference given by Linnaeus, who did not see Sloane's specimen from which the plate was prepared, until after the publication of the first edition of *Species Plantarum* (Linnaeus, 1753). Sloane's plate is finely detailed and clearly it is this species. No other Jamaican species of the genus has such conspicuous secondary bracts and such a large inflorescence as *C. odoratus*.

⁴CYPERUS CORRELLII (T. Koyama) Tucker, comb. nov., based on *Torulinium correllii* T. Koyama, Brittonia 28:252. 1976.

Cyperus odoratus, as recognized here, is readily recognized by its cylindrical spikelets in which the corky rachilla of the mature spikelet disarticulates at the base of each scale. Thus the mature spikelet breaks up into segments each consisting of a scale and an internode of the rachilla clasping the achene with its corky wings. Following is the synonymy of *C. odoratus* in Mexico and Central America.

CYPERUS ODORATUS L.

- C. odoratus* L., Sp. Pl. 1:46. 1753. TYPE: Sloane's plate in Voy. Jam. Nat. Hist. 1:116. t. 74, fig. 1, 1707 (see Exell, 1944). *Torulinium odoratum* (L.) Hooper, Kew Bull. 26:579. 1972.
- C. ferax* L. C. Rich., Act. Soc. Hist. Nat. Paris 1:106. 1792. TYPE: Guiana. Cayenne, Leblond (HOLOTYPE: G, not seen; microfiche at GH!). *Mariscus ferax* (L. C. Rich.) C. B. Clarke, in J. D. Hook. Fl. Brit. India 6:624. 1894. *Torulinium ferax* (L. C. Rich.) Urb., Symb. Antill. 2:165. 1900.
- C. speciosus* Vahl, Enum. pl. 2:364. 1806. TYPE: not located; type locality: "America septentrionalis." *C. ferax* ssp. *speciosus* (Vahl) Kükenth., Pflanzenreich 4(20):619. 1936.
- C. buenkei* Presl, Reliq. Haenk. 1:172. 1828. TYPE: MEXICO. Haenke (PR?).
- C. ebrenbergii* Kunth, Enum. pl. 2:89. 1837. TYPE: VIRGIN ISLANDS. St. Thomas, Ehrenberg 77 (ISOSYNTYPE: HAL!).
- Diclidium aciculare* Schrad. ex Nees, Fl. bras. 2(1):55. 1842. TYPE: BRAZIL. Bahia, Martius (M). *C. acicularis* (Nees) Steud., Syn. Cyp. 45. 1854.
- C. macrocephalus* Liebm., Mexic. halvgr. 33. 1850. TYPE: MEXICO. Veracruz, Río Nautla at Pital, Liebmann 14367 (HOLOTYPE: CI; ISOTYPES: GH! HAL! K! LL! photo:FI MICH!). *Torulinium macrocephalum* (Liebm.) Koyama, Phytologia 29:74. 1974.
- C. cubanus* Liebm., Mexic. halvgr. 34. 1850. TYPE: CUBA. near Havana, "in uliginosis," April 1845, Liebmann 14355 (HOLOTYPE: CI!).
- C. rufinus* Liebm., Mexic. halvgr. 34. 1850. TYPE: MEXICO. Puebla, Tehuacán, S. Lorenzo, "ad ripas fluvii," Dec. 1842, Liebmann 14373 (HOLOTYPE: CI!).
- C. sanctae-crucis* Liebm., Mexic. halvgr. 35. 1850. TYPE: VIRGIN ISLANDS. St. Croix, Lagunen ved Frederiksstad, Oersted 14374 (HOLOTYPE: CI!).
- C. granadinus* Liebm., Mexic. halvgr. 36. 1850. TYPE: NICARAGUA. Granada, June, Oersted 14363 (HOLOTYPE: CI!).
- C. oerstedii* Liebm., Mexic. halvgr. 36. 1850. TYPE: NICARAGUA. Segovia, January 1848, Oersted 14372 (HOLOTYPE: CI!).
- C. forsterum* Liebm., Mexic. halvgr. 37. 1850. TYPE: MEXICO. Oaxaca, near Tehuantepec by Hacienda de Sta. Cruz, "in fossis," December 1842, Liebmann 14359 (HOLOTYPE: CI; ISOTYPES: GH! K!).
- C. fragilis* Liebm., Mexic. halvgr. 38. 1850. TYPE: MEXICO. Veracruz, coast region by Paso de Doña Juana, Feb. 1841, Liebmann 14360 (HOLOTYPE: CI; ISOTYPE: K!).
- C. engelmannii* Steud., Syn. Cyp. 47. 1854. TYPE: U.S.A. Illinois, Cahokia, Sept. 1845, Engelmann (HOLOTYPE: P?; ISOTYPE: GH!). *C. ferax* ssp. *engelmannii* (Steud.) Kükenth., Pflanzenreich 4(20):620. 1936.
- C. oxycarioides* Britton, Bull. Torrey Bot. Club 11:86. 1884. TYPE: U.S.A. Texas, valley of the lower Rio Grande, Buckley s.n. (HOLOTYPE: NY!).
- C. eggersii* Boeck., Cyp. nov. 1:53. 1888. TYPE: DOMINICAN REPUBLIC. Santo Domingo, near Batey on Río Yasia, 23 June 1887, Eggers 2627 (HOLOTYPE: B!). *Torulinium eggersii* (Boeck.) C. B. Clarke, Symb. Antill. 2:56. 1900.

ACKNOWLEDGMENTS

I would like to thank Prof. Robert L. Wilbur for his support and advice in the present study, the Gray Herbarium Library for access to literature, and the curators of the following herbaria for sending specimens: A, B, BH, BM, BR, C, CAS, CGE, CR, CU, DS, E, F, FLAS, GH, HAL, K, LCU, LL, M, MICH, MO, MSC, NY, PENN, PH, PMA, PRC, S, TEX, US, WIS, and Z.

REFERENCES

- AYERS, B. 1946. The genus *Cyperus* in Mexico. Cath. Univ. Amer. Biol. Stud. 1. xi + 103 pp.
- CORRELL, D. S. and M. C. JOHNSTON. 1970. Manual of the vascular plants of Texas. Texas Res. Found., Renner, Tex. xv + 1881 pp.
- DENTON, M. F. 1978. A taxonomic treatment of the Luzulae group of *Cyperus*. Contr. Univ. Mich. Herb. 11:197-271.
- EXELL, A. W. 1944. Catalogue of the vascular plants of S. Toré. London: British Museum. xi + 428 pp.
- FERNALD, M. L. 1950. Gray's manual of botany, 8th ed. New York: American Book Co. lxiv + 1632 pp.
- KERN, J. H. 1974. *Cyperus*. In Flora Malesiana. 7(3):592-661.
- KOYAMA, T. 1978. Cyperaceae. In R. A. Howard, ed., Flora of the Lesser Antilles. 3:220-320.
- KÜKENTHAL, G. 1935-36. *Cyperus*. In A. Engler & L. Diels, eds., Das Pflanzenreich 4(20):1-671.
- LINNAEUS, C. 1753. Species plantarum. Stockholm. 1200 pp.
- O'NEILL, H. T. 1940. The sedges of the Yucatan Peninsula. Carneg. Inst. Wash. Misc. Papers 19.
- STANDLEY, P. C. 1931. The Cyperaceae of Central America. Fieldiana Bot. 8(4):239-292.
- . 1938. The flora of Costa Rica (*Cyperus*). Fieldiana Bot. 18:96-100.
- TUCKER, G. C. 1983. The taxonomy of *Cyperus* (Cyperaceae) in Costa Rica and Panama. Syst. Bot. Monogr. 2:1-85.
- VOSS, E. G. 1972. Michigan flora, pt. 1. Bloomfield Hills, MI: Cranbrook Inst. of Science.