CYPERUS FLAVICOMUS (CYPERACEAE), LONG MISNAMED *C. MACROSTACHYOS*: A COMPREHENSIVE TAXONOMIC REASSESSMENT WITH ANNOTATED SYNONYMY AND VOUCHER-BACKED GLOBAL DISTRIBUTION

Aidan D. Ross and Jason K. Norsworthy

University of Arkansas
Department of Crop, Soil, and Environmental Sciences
1354 W Altheimer Dr., Fayetteville, Arkansas 72704, U.S.A.
aidandr@uark.edu; jnorswor@uark.edu

ABSTRACT

The pantropical annual flatsedge widely known as *Cyperus macrostachyos* Lam. (Cyperaceae; *Cyperus* subg. *Cyperus*, former segregate genus *Pycreus*) has been described under no fewer than 30 names over the past two centuries, variously treated as one or two species, with no substantive consensus on circumscription or nomenclature. In North America, the species is instead recognized as *C. flavicomus* Michx. To resolve these discrepancies, we examined the protologues and, where available, original type material for all names currently or historically synonymized with *C. macrostachyos* s.l., supplemented by an extensive survey of digitized collections ascribed to the species and of broader *Pycreus* material from Africa and South Asia (ca. 2,000 specimens from 130 herbaria in total). We report three principal findings. First, the morphological variation historically used to separate the species into two taxa is attributable to characters that are either environmentally plastic or maturity-dependent, and does not warrant recognition of more than one species. Second, examination of the holotype and holotype fragment of *C. macrostachyos* reveals that the material is not conspecific with the pantropical species to which it has been applied since Hooper and Raynal (1969), but corresponds in all observable characters to the South Asian endemic *C. puncticulatus* Vahl. The "Ex Africa" locality cited by Lamarck (1791) could not be corroborated by any material among the extensive African collections surveyed; we render the type citation as "Uncertain locality ('Ex Africa' teste Lamarck 1791)" to reflect this. Third, the correct name for the pantropical species is *C. flavicomus* Michx. (1803)—first reinstated by Tucker (1985), here independently confirmed and extended to encompass the full synonymy. Conservation of *C. puncticulatus* Vahl against *C. macrostachyos* Lam. is recommended under Art. 14 of the ICN; a formal proposal will be submitted to Taxon. An annotated synonymy, revised description, and voucher-backed global distribution for *C. flavicomus* Michx. and lectotype designations for eleven names are provided.

RÉSUMÉ

La cypéracée annuelle pantropicale largement connue sous le nom de *Cyperus macrostachyos* Lam. (Cyperaceae ; *Cyperus* subg. *Cyperus*, l'ancien genre ségrégé *Pycreus*) a été décrite sous plus de 30 noms au cours des deux derniers siècles, traitée tantôt comme une espèce unique, tantôt comme deux, sans consensus substantiel sur sa circonscription ni sa nomenclature. En Amérique du Nord, l'espèce est reconnue sous le nom de *C. flavicomus* Michx. Afin de résoudre ces divergences, nous avons examiné les protologues et, lorsqu'ils étaient disponibles, les matériaux types originaux de tous les noms actuellement ou historiquement synonymisés avec *C. macrostachyos* s.l., complétés par un examen approfondi des collections numérisées attribuées à l'espèce ainsi que d'un matériel élargi de *Pycreus* d'Afrique et d'Asie du Sud (environ 2 000 spécimens provenant de 130 herbiers au total). Nous présentons trois conclusions principales. Premièrement, la variation morphologique historiquement utilisée pour séparer l'espèce en deux taxons est attribuable à des caractères soit liés à la plasticité environnementale, soit dépendants du stade de maturité, et ne justifie pas la reconnaissance de plus d'une espèce. Deuxièmement, l'examen de l'holotype et du fragment d'holotype de *C. macrostachyos* révèle que ce matériel n'est pas conspécifique de l'espèce pantropicale à laquelle il est rattaché depuis Hooper et Raynal (1969), mais correspond, dans tous les caractères observables, à l'espèce endémique d'Asie du Sud *C. puncticulatus* Vahl. La localité « Ex Africa » citée par Lamarck (1791) n'a pu être corroborée par aucun matériel parmi les vastes collections africaines examinées ; nous formulons la citation du type comme « Localité incertaine ('Ex Africa' teste Lamarck 1791) » afin de refléter ce constat. Troisièmement, le nom correct pour l'espèce pantropicale est *C. flavicomus* Michx. (1803) —d'abord rétabli par Tucker (1985), ici indépendamment confirmé et étendu à la synonymie complète. La conservation de *C. puncticulatus* Vahl contre *C. macrostachyos* Lam. est recommandée au titre de l'Art. 14 du CIN ; une proposition formelle sera soumise à Taxon. Une synonymie annotée, une description révisée, une distribution mondiale étayée par des spécimens-témoins pour *C. flavicomus* Michx. et des désignations de lectotypes pour onze noms sont fournies.

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RESUMEN

A ciperácea anual pantropical amplamente conhecida como *Cyperus macrostachyos* Lam. (Cyperaceae; *Cyperus* subg. *Cyperus*, o antigo gênero segregado *Pycreus*) foi descrita sob mais de 30 nomes ao longo dos últimos dois séculos, tratada ora como uma única espécie, ora como duas, sem consenso substantivo quanto à sua circunscrição ou nomenclatura. Na América do Norte, a espécie é reconhecida como *C. flavicomus* Michx. Para resolver essas discrepâncias, examinamos os protólogos e, quando disponíveis, os materiais-tipo originais de todos os nomes atual ou historicamente sinonimizados com *C. macrostachyos* s.l., complementados por um levantamento extenso de coleções digitalizadas atribuídas à espécie e de material mais amplo de *Pycreus* da África e do sul da Ásia (ca. 2.000 espécimes de 130 herbários no total). Apresentamos três conclusões principais. Primeiro, a variação morfológica historicamente utilizada para separar a espécie em dois táxons é atribuível a caracteres ambientalmente plásticos ou dependentes do estágio de maturação, e não justifica o reconhecimento de mais de uma espécie. Segundo, o exame do holótipo e do fragmento de holótipo de *C. macrostachyos* revela que esse material não é coespecífico da espécie pantropical à qual tem sido aplicado desde Hooper e Raynal (1969), mas corresponde, em todos os caracteres observáveis, à espécie endêmica do sul da Ásia *C. puncticulatus* Vahl. A localidade "Ex Africa" citada por Lamarck (1791) não pôde ser corroborada por nenhum material dentre as extensas coleções africanas examinadas; formulamos a citação do tipo como "Localidade incerta ('Ex Africa' teste Lamarck 1791)" para refletir esse fato. Terceiro, o nome correto para a espécie pantropical é *C. flavicomus* Michx. (1803)—primeiramente restabelecido por Tucker (1985), aqui independentemente confirmado e estendido para abranger a sinonímia completa. A conservação de *C. puncticulatus* Vahl contra *C. macrostachyos* Lam. é recomendada sob o Art. 14 do CIN; uma proposta formal será submetida ao Taxon. São fornecidas uma sinonímia anotada, uma descrição revisada, uma distribuição global respaldada por espécimes-testemunho para *C. flavicomus* Michx. e designações de lectótipos para onze nomes.

Key Words: Cyperaceae, *Cyperus flavicomus* Michx., *Cyperus macrostachyos* Lam., synonymy, morphology, distribution, lectotype designation.

INTRODUCTION

The species commonly known as *Cyperus macrostachyos* Lam. (sensu Hoenselaar et al. 2010) is a facultative wetland annual flatsedge occurring throughout the Old World tropics and Americas (Kükenthal 1935–1936; Tucker 1983; Early et al. 2024). Robust individuals may exceed a meter in height with fully decompound inflorescences (Fig. 1: A, B), while stressed or late-season plants may stand barely a third as tall, with more compact, few-rayed compound anthelodia (Fig. 1: C, D). However, the species can always be readily distinguished by its diagnostic glumes (synonym, floral scales): non-overlapping at maturity, and with broad whitish-hyaline margins (Tucker 1983; Haines & Lye 1983; Hoenselaar et al. 2010).

Historically a species of little note in the United States flora, it was thrust into prominence in 2014 when found infesting rice (*Oryza sativa* L.) in Arkansas, U.S.A. (det. C.T. Bryson, *C.E. Wilson Jr. #s.n.,* [ANHC008726]). Efforts to compile existing knowledge on the species have been hampered by a fundamental discrepancy. Despite the accepted status of the name *C. macrostachyos* Lam. (Hoenselaar et al. 2010; Cyperaceae Working Group 2025; POWO 2026), a parallel taxonomy is currently followed for the species in North America under the name *C. flavicomus* Michx. (sensu Tucker 1985) (PLANTS Database 2026).

Investigation into this discrepancy revealed a nomenclatural history far more tangled than the simple two-name problem might suggest: the species has been described under no fewer than 30 names from numerous countries over the past two centuries. Some have treated it as a single species (Bentham & Mueller 1878; Wild & McEwen 1961; Hooper 1972; Hoenselaar et al. 2010; Mesterházy et al. 2022), while others have treated it as two species divided along inconsistent morphological lines upon which no two authors have completely agreed (Boeckeler 1868; Clarke 1886; Kükenthal 1935–1936; Haines & Lye 1983). The name currently in use throughout most of its range—*C. macrostachyos* Lam. (1791)—was completely absent from literature until resurrection by Hooper and Raynal (1969), later rejected by the only modern author documented to have personally examined its type (Tucker 1985), and yet remains widely in use. *C. flavicomus* Michx.—the name accepted in North America—was relegated as a synonym of an unrelated species for nearly a century until reinstatement by the same author (Tucker 1985). This is but a glimpse of the extensive historical confusion surrounding the circumscription and nomenclature of this species (Kunth 1837; Boeckeler 1868; Bentham & Mueller 1878; Kükenthal 1935–1936; Haines & Lye 1983); a comprehensive reassessment is clearly warranted.

To resolve these discrepancies and standardize the scientific name for this species, the protologues and, when available, original type material for any names currently or historically treated as synonyms of *C.*

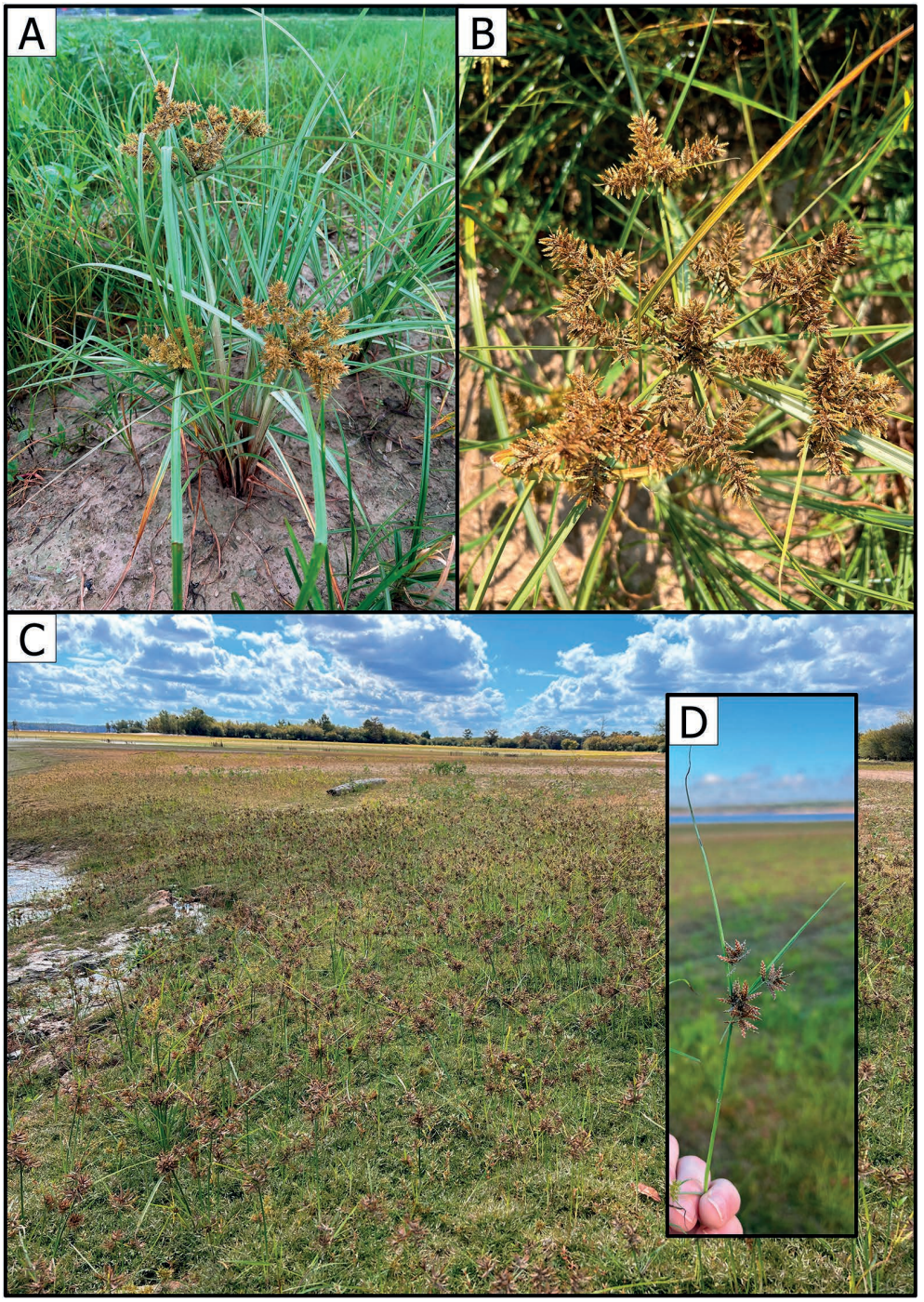


Fig. 1. *Cyperus flavicomus* Michx. **A.** A large individual (ca. 1 m tall) in the field margin of an Arkansas rice paddy, 22 July 2024. **B.** An example of a decompound inflorescence in an individual from a neighboring field, 28 July 2024. **C.** A late-season population (ca. 30–40 cm tall) from a drawdown mudflat at Grenada Lake, Mississippi, 18 October 2025 (*A.D. Ross & C.T. Bryson #s.n.*, [AWS-2025- GREN]). **D.** An example of a more compact, few-rayed compound inflorescence from the pictured Grenada Lake population. Photos: A.D. Ross.

macrostachyos s.l. were thoroughly examined. We report three principal findings: the morphological variation within this species does not warrant its separation into multiple taxa; the correct name for this species is *C. flavicomus* Michx.; and the type of *C. macrostachyos* Lam. does not belong to this species, but rather to the closely related *C. puncticulatus* Vahl.

MATERIALS AND METHODS

Nomenclatural decisions in this work follow the International Code of Nomenclature for algae, fungi, and plants (Madrid Code, Turland et al. 2025). For names lacking a previously designated lectotype, one was selected from the materials cited in the respective protologue; justifications for each selection are provided following the synonymy. Herbarium abbreviations follow the Index Herbariorum (Thiers 2026 [continuously updated]; available at https://sweetgum.nybg.org/science/ih/).

For all names treated in this study, we sought to examine the original type material and the published protologue. Where type material was unavailable for examination, the protologue and published descriptions by any authors documented to have examined the type firsthand were consulted instead. Protologues were located with the assistance of Kükenthal's (1935–1936) monograph of Cyperaceae, Govaerts and Simpson's (2007) world checklist of Cyperaceae, and Plants of the World Online (POWO, https://powo.science.kew.org/). All original texts were accessed digitally through the Biodiversity Heritage Library (https://www.biodiversitylibrary.org/) and the Internet Archive (https://archive.org/), physically through the University of Arkansas Interlibrary Loan Service, or purchased in print by the authors. Herbarium specimens were examined from digital images accessed chiefly through the Kew Data Portal (https://data.kew.org/), JSTOR Global Plants Database (https://plants.jstor.org/), iDigBio (https://www.idigbio.org/portal/search), Southeast Regional Network of Expertise and Collections (SERNEC, https://sernecportal.org/portal/index.php#), Plantentuin Meise Digital Herbarium (https://www.botanicalcollections.be/#/en/search/specimen), Linnean Online (https://linnean.access.preservica.com/?s=), Smithsonian Institution Botany Collections (https://collections.nmnh.si.edu/search/botany/), Atlas of Living Australia (https://ala.org.au/), speciesLink (https://specieslink.net/search/), Botanical Survey of India (https://bsi.gov.in/), and the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/). Le Réseau national des collections naturalistes (Récolnat) and the MNHN Data Portal were available prior to a cyberattack in July 2025 that rendered both inaccessible at the time of writing; as such, the P holdings examined here were limited almost entirely to those available through GBIF.

Molecular phylogenetic analyses have shown that species formerly placed in the segregate genus *Pycreus* do not represent a monophyletic group, but rather are nested within a monophyletic clade of C_4, chlorocyperoid species inside an otherwise paraphyletic *Cyperus* (Larridon et al. 2013, 2014). The genus *Pycreus* was consequently subsumed within *Cyperus* subg. *Cyperus,* whose infrageneric classification has not yet been resolved; still, *Pycreus* spp. can be morphologically distinguished within the subgenus due to the distinctive inflorescence characters of the former segregate genus. Lacking an accepted infrageneric name for the former *Pycreus* species, we refer to them informally as "*Pycreus*" throughout this work.

In addition to the relevant type materials, the above databases were surveyed between January and March 2026 for global collections filed under any name currently or historically synonymized with *C. macrostachyos* s.l., as well as for broader collections of *Pycreus* from Africa and South Asia. The survey was restricted to *Pycreus* based on the observable characters presented by the holotype and holotype fragment of *C. macrostachyos* Lam., as described in detail in the following discussion. Published accounts of African Cyperaceae, principally Haines and Lye (1983) and Hoenselaar et al. (2010), were also consulted. Approximately 2000 specimens from 130 herbaria were examined in total (Appendices 1, 2, 3). For practicality, collections from the broader survey were included in Appendix 3 only if explicitly referenced in the discussion; the full scope of the survey encompassed extensive available digitized materials of the subgenus from the regions indicated.

Field-collected material from weedy populations across rice-producing regions of Arkansas and Missouri has been submitted to the University of Arkansas Weed Science Program regularly since 2023 by growers, consultants, and extension agents for herbicide resistance screening. These submissions were supplemented by personal collections from rice fields in Arkansas and from seasonally dewatered mudflats at Grenada Lake and Enid Lake in Mississippi (assisted by Dr. Charles T. Bryson). Because the primary purpose of these collections is weed science research, samples are generally processed into threshed seed shortly after collection and identification; viable seed and cleaned achenes are maintained in cold storage at the University of Arkansas Division of Agriculture Weed Science Program, Fayetteville, Arkansas, rather than deposited in a recognized herbarium. Although not stored as traditional voucher specimens, this material was useful for species description, figure preparation, and documentation of distribution—no taxonomic conclusions were based on it alone. For citation purposes, these collections are designated with the prefix AWS (Arkansas Weed Science), year, and accession number, separated by hyphens (e.g., AWS-2023-046; see Appendix 1).

Specimen citations follow the format: *Collector #number,* [BARCODE] (e.g., *Schimper #1551,* [K000363005]). Institution barcodes are presented exactly as given by their respective institutions, and always within brackets. Where the barcode includes the herbarium code (e.g., K: [K000463885], P: [P00667331]), no separate herbarium abbreviation is given. For institutions not including their herbarium code within barcodes, the herbarium code is provided within the brackets immediately preceding the institution barcode, separated by a colon (e.g., [US:2719074]). Dashes or spaces are included only as present in the institution barcode (e.g., [B 10 0296611], [S13-17825]).

An exclamation mark (!) following a specimen citation indicates that the specimen was personally examined by the authors. Unless explicitly stated otherwise, all specimens were examined digitally. Specimens for which available images were insufficient for reliable determination were excluded from consideration, except where they constituted the only extant imagery of an original type specimen. High-resolution images of the holotype-bearing sheet of *C. flavicomus* Michx. (*A. Michaux #s.n.,* [P00667331]), not previously available digitally, were kindly provided directly by the Muséum National d'Histoire Naturelle in Paris. Images of the *C. macrostachyos* holotype and holotype fragment were retrieved from the MNHN Data Portal prior to the July 2025 cyberattack. Type images for other names housed at P were accessed through JSTOR Global Plants or GBIF.

From the verified specimen records compiled in Appendices 1 and 2, distribution maps were generated using a custom D3.js (v7; Bostock et al. 2011) visualization developed for this study. The visualization code was written by Claude Opus 4.6 (Anthropic PBC) under the direction and specifications of the first author, who designed the data structure, selected the basemaps and color scheme, verified all FIPS and name matching between specimen records and basemap features, and validated the final outputs against the source records. Records were aggregated to the U.S. county level (by Census FIPS code) for the United States map and to the country level for the global map; for Australia, Brazil, India, Mexico, and the United States, records were further aggregated to first-order administrative divisions for a combined subnational overlay. The U.S. county basemap was the pre-projected Albers USA counties-albers-10m TopoJSON from us-atlas (https://github.com/topojson/us-atlas; derived from U.S. Census Bureau TIGER/Line cartographic boundary files, https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html), and the global country basemap was the countries-110m TopoJSON from world-atlas (https://github.com/topojson/world-atlas; derived from Natural Earth 1:110m cultural vectors, https://www.naturalearthdata.com). State-level boundaries for Australia, Brazil, India, and Mexico were obtained from publicly available community GeoJSON repositories (https://github.com/tonywr71/GeoJson-Data, https://github.com/codeforamerica/click_that_hood, https://github.com/geohacker/india, https://github.com/angelnmara/geojson, respectively); U.S. state polygons were from a public-domain dataset derived from U.S. Census Bureau TIGER/Line shapefiles. River features for the U.S. county map were sourced from Natural Earth 1:10m physical vectors (https://github.com/nvkelso/natural-earth-vector). All subnational boundary files were geometrically simplified prior to embedding to reduce file size.

RESULTS AND DISCUSSION

Within *Pycreus,* there are two species characterized by broadly white-margined glumes—one a nomenclaturally stable South Asian endemic, and the other a taxonomic puzzle of nearly two centuries' standing. The first—known for its more imbricated glumes and superficial resemblance to *C. procerus* Rottb. (Clarke 1886; Kern 1974; Koyama 1977)—has been consistently recognized as a single, coherent taxon under the name *C. puncticulatus* Vahl.

The second—widely distributed throughout the Old World tropics and Americas—has been described under many different names, including *C. flavicomus* Michx. from the United States (Michaux 1803), *C. tremulus* Poir. from Madagascar (Poiret 1806), *P. albomarginatus* Mart. & Schrad. ex Nees from Brazil (Nees 1842), *C. hochstetteri* Nees ex Krauss from Sudan (Krauss 1845), *C. ornatissimus* F. Muell. from Australia (Mueller 1874), *C. patuliflorus* Boeck. from India (Boeckeler 1868), and *C. macrostachyos* Lam. (Lamarck 1791), among others. The result has been considerable confusion regarding its circumscription. Compounding this confusion, the prevailing view throughout the late 19th and much of the 20th century was that these collections represented not one, but two species, divided along various morphological lines by different authors—no two of whom agreed precisely on which characters were diagnostic or where the boundary fell. George Bentham (Bentham & Mueller 1878) was the first to formally unite these collections as a single taxon—a position that was either outright rejected or ignored entirely until Wild and McEwen (1961), Hooper (1972), and Hoenselaar et al. (2010) independently reached the same conclusion much later. To avoid prejudicing the nomenclatural question addressed herein, we refer to this species concept hereafter as "Bentham's flatsedge."

One variable species?—The characters historically cited in support of separating Bentham's flatsedge into two species fall into two broad categories. The first—overall habit, glume morphology, and stamen number—involve variation that is either straightforwardly environmental or too continuous to carry diagnostic weight. The second—inflorescence ramification, achene (synonym, nutlet) dimensions, achene color, and spikelet width—requires more detailed treatment, as these characters involve developmental processes whose effects on specimen appearance have not previously been addressed in the literature on this species. The following analysis addresses each of these characters in sequence, then turns to the identity of the names applied to Bentham's flatsedge and the nomenclatural consequences of their resolution.

Habit.—The first character employed in support of separating Bentham's flatsedge into two species was overall habit—the general size and stature of the plant. Nees (1842), in describing *P. sabulosus* alongside *P. albomarginatus,* conceded an affinity between the two in their glumes and achenes but maintained that the plants themselves were as different as could be: "Quoad squamarum et caryopsidum indolem aliqua affinitas intercedit hanc inter et praecedentem speciem; in reliquis tamen, ut habitu toto, quam maxime ab illa recedit" (as regards the nature of the glumes and achenes, some affinity exists between this and the preceding species; in all other respects, however, and especially in overall habit, it departs from it as much as possible). At first glance, this seems a palpable difference—the robust, solitary, tall-culmed *P. albomarginatus* set against the wiry, caespitose, diminutive *P. sabulosus*. But Elliott's (1821) observations regarding the species tell a different story: "In bogs it becomes a large plant, 2–3 feet high, thick and succulent; in dry soils, even where not sandy, it rarely exceeds 12–15 inches in height." Over a century later, Blatter and McCann (1934) documented the same plasticity in Indian populations of the species: "When on 'dry' ground a much shorter and robust plant, when in water grows taller with larger umbels." A striking illustration of this environmental influence on habit can be seen by comparing one of Elliott's Lowcountry specimens held at K (*Elliott #s.n.,* [K002544103]) with Wright's New Mexican collection (*C. Wright #1965*, [K002544100]), described by Torrey (1859) as "smaller than the usual form of this species … but in other respects there is no essential difference" (Fig. 2). This same effect is almost certainly what Martius' own collections presented to Nees. His *P. albomarginatus* material came from "in ripa fluminis S. Francisci ad Joazeiro prov. Bahiensis"—the banks of the Rio São Francisco, a perennial river with substantial alluvial floodplains that would have provided continuous access to moisture and nutrients, producing the robust individuals Nees described. His *P. sabulosus* material came from "in campis arenosis udis juxta lacum Coari, provinciae fluminis Nigri"—moist sandy plains near Coari



Fig. 2. Example of growth habit differences in *Cyperus flavicomus* Michx. across environments. **A.** From the coastal plain of South Carolina or Georgia (Lowcountry), *Elliott #s.n.*, [K002544103]. **B.** From New Mexico, *C. Wright #1965*, [K002544100].

Lake in the Amazonian interior, nutrient-poor sandy substrate that, despite adequate moisture, would consistently produce smaller, less robust plants. Two habitats, two habits, one species.

More sharply distinguishing the two, Nees described *P. albomarginatus* as having a "culmus tuberascens" and explicitly marked its protologue with the astrological symbol for Jupiter (♃)—denoting a perennial life cycle (Steudel 1821)—while *P. sabulosus* was "ut videtur annua." This, too, is an artifact of the same environmental effect. A vigorous individual of Bentham's flatsedge presents several features that could easily be mistaken for perenniality. The culm base is fleshy to the touch, and the lower quarter to half is loosely covered by membranous reddish-brown leaf bases that split and shred as the plant grows—giving the base a disheveled, layered appearance that could readily suggest a perennial organ system. The marcescent leaves, slow to decompose, could be mistaken for remnants of previous seasons' growth. And the habit of forming new culms that pierce upward through the old leaf bases could be misinterpreted as evidence of a "tuberous culm base"—a true example of which can be seen in *C. strigosus* L., a genuinely perennial species whose corm-like base looks quite different upon excavation but which shares that superficial appearance of new shoots emerging from old tissue. Taken together, these features make it easy to mistake a robust annual like Bentham's flatsedge for a perennial in the field—similar observations have led to particularly large specimens of the annual *C. iria* L. being reported as perennial on occasion (cf. Haines & Lye 1983).

Other major authors have also variously published or speculated that the species was a perennial (Kunth 1837; Steudel 1855; Bentham & Mueller 1878). Michaux himself did not officially publish *C. flavicomus* with the perennial symbol, but did mark the holotype-bearing sheet [P00667331] with a large "♃"—whether confidently or tentatively is unclear. Modern reports of Bentham's flatsedge as a rhizomatous perennial are entirely limited to rumor or misidentified individuals of *C. longistolon* Peter & Kük. (= *C. chrysanthus* Boeck., fide Browning et al. 2020 apud POWO 2026), a true perennial with long-creeping stolons that produces

superficially similar white-margined glumes and can be found growing alongside Bentham's flatsedge in certain parts of tropical Africa (cf. Haines & Lye 1983). Robust habit, fleshy culm bases, apparent perenniality, caespitose growth—all of the characters Nees used to distinguish *P. albomarginatus* from *P. sabulosus*—reduce to environmental variation, a conclusion consistent with the treatment of Tucker (1985), who examined the holotypes of both names and treated them as synonyms.

Glume color and apex.—The color and shape of the glume have been used by several authors to distinguish what they perceived as distinct taxa within Bentham's flatsedge. Small (1913) separated *C. flavicomus* from *C. hochstetteri* in part on glume characters, describing the former with "scales oblong, obtuse, thin, dull yellowish brown" and the latter with "scales broadly ovate, deep chestnut color … rather blunt." Clarke (1886), by contrast, noted variation in the American form—"Forma '*albo-marginati,*' sp. Nees, in America meridionali indigena est; differt a formis gerontogeis nervo medio glumae sub apice vix ac ne vix excurrente," the keel sometimes scarcely extending beyond the apex—but did not consider it sufficient grounds for separation, retaining it within his broader concept of *C. hochstetteri*. If the most prolific Cyperaceae taxonomist of the late nineteenth century examined the glume variation firsthand and dismissed it, the burden of proof falls heavily on those who would elevate it to a diagnostic character.

Glume color varies continuously across the range of the species and correlates with growing conditions rather than taxonomic identity. Later-season plants from seasonally dewatered mudflats, such as our collections from Mississippi, correspond closely to *C. hochstetteri* sensu Small (1913) (glumes more nearly ovate, deep chestnut color); plants from cultivated rice fields, such as our collections from Arkansas and Missouri, correspond more closely to his *C. flavicomus* (glumes more nearly oblong, dull yellowish-brown). The two forms intergrade completely, and neither is geographically fixed; when we grew plants in a greenhouse from seed collected from Grenada Lake, Mississippi (*A.D. Ross & C.T. Bryson #s.n.*, [AWS-2025-GREN]), the inflorescences of the progeny were markedly lighter in color than those of the parent collection (Fig. 3).

The problem is compounded by preservation: Blatter and McCann (1934) observed that spikelets of Bentham's flatsedge are "brown, frequently becoming reddish in the herbarium," and cautioned of *Cyperus* in general that "the colour of the glumes like that of the wing of the rhachilla is a dangerous character and should be used with circumspection, particularly in herbarium material." Given that nearly every taxonomic treatment of the species has been based primarily on dried specimens, this artifact alone could account for much of the apparent disagreement in the literature. The range of color descriptions confirms this, variably described as "yellowish-brown" (Torrey 1836), "flavo-rufescentes vel fulvae" and "rufescentes" (Kükenthal 1935–1936), "yellow or ruddy brown" (Clarke 1894), "light brown to reddish brown" (Tucker 1983), "golden or reddish brown" (Haines & Lye 1983), "(golden-)yellow, (golden-)brown to reddish brown" (Hoenselaar et al. 2010), etc. Every treatment describes a different slice of the same continuum, and no two authors draw the diagnostic line in the same place.

The glume apex character is less straightforward. In fresh material, glumes of Bentham's flatsedge have a hyaline margin extending beyond the green keel, giving the apex a rounded, obtuse appearance and the glume a broadly obovate outline. The width of this margin can vary among populations and with growing conditions—some glumes bear a particularly broad, conspicuous border while others have a somewhat narrower one—but in all cases it is whitish-hyaline and conspicuous.

Especially in older collections, this margin appears prone to fraying or erosion with age, handling, or weathering—progressively exposing the keel tip and producing the appearance of a narrower, more acute apex. Compounding the problem across treatments, there is little standardization in how glume shape has been assessed: some authors appear to have described the entire glume removed and flattened, while others described the glume as it presents on the spikelet, folded along the keel—the same glume appearing broadly ovate in the first case and more narrowly oblong in the second. Between possible margin erosion, inconsistent methodology, and genuine environmental variation, a considerable range of apex descriptions—somewhat emarginate (Torrey 1836), obtuse (Elliott 1821), acute (Small 1913), etc.—has been applied to specimens of

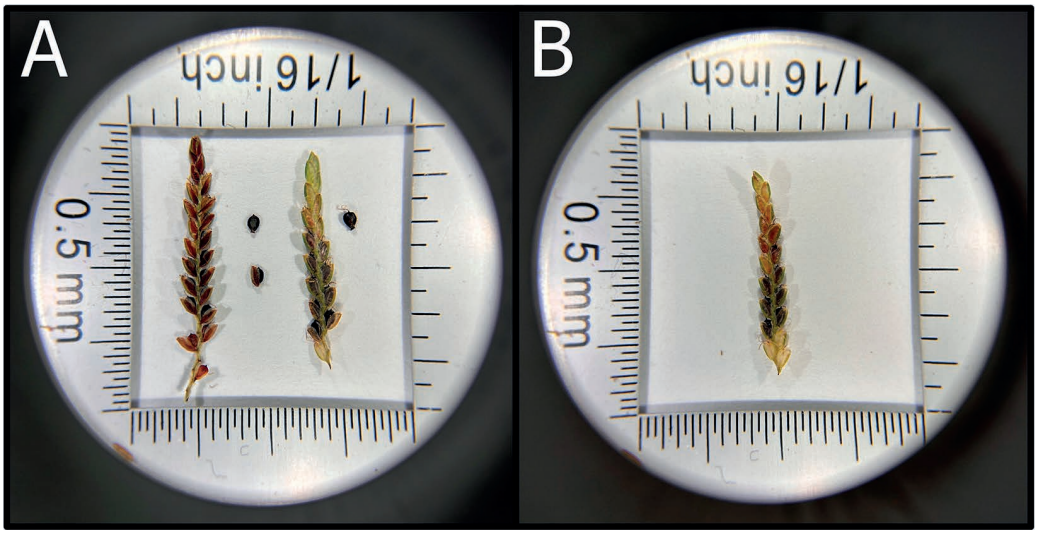


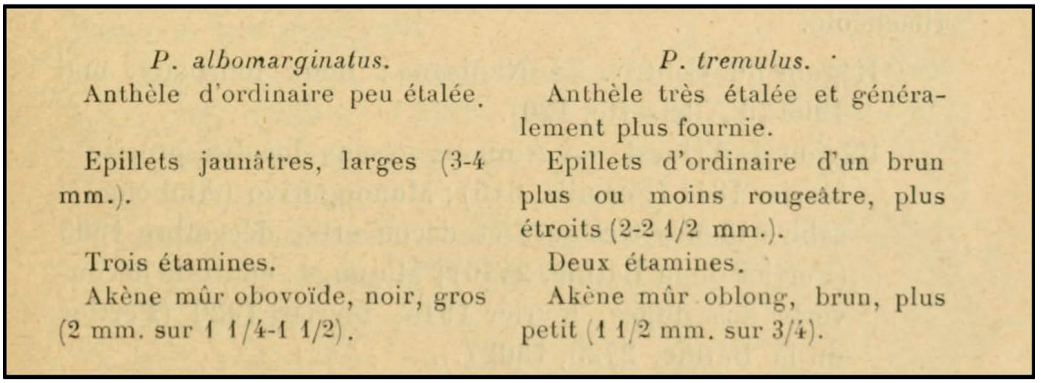
Fig. 3. Spikelets of *Cyperus flavicomus* Michx. selected to represent discussed glume variation. A. Left: a spikelet and isolated achenes from an individual collected at Grenada Lake, Mississippi, 18 October 2025 (*A.D. Ross & C.T. Bryson #s.n.*, [AWS-2025-GREN]); Right: a spikelet and isolated achene from an individual grown from seed of the Grenada Lake collection in a Fayetteville, Arkansas greenhouse, 24 March 2026. B. Glume shape and color variation within a single spikelet from an individual collected at Grenada Lake. Photos: A.D. Ross.

this single species; this may explain why Nees (1842) described the glumes of one of his taxa as ovate and the other as oblong.

Kükenthal (1935–1936) described the glumes of his two species in largely overlapping terms—"Squamae … ovatae vel subobovatae" for *C. albomarginatus* and "squamae … subobovatae obtusae" for *C. tremulus*. Chermezon (1919) cited color as differing between his two species but did not distinguish them by shape. Most tellingly, Haines and Lye (1983) described the glumes of both their subspecies (*C. macrostachyos* ssp. *macrostachyos* and ssp. *tremulus*) in virtually identical terms, making no distinction between the two ("obovate, golden or reddish brown with a usually distinct green midrib and a very distinct about 0.3 mm wide white hyaline margin; apex rounded and the midrib stopping at the white marginal border" versus "obovate, golden or reddish brown with green not excurrent midrib and a very distinct 0.2–0.3 mm wide white marginal border; apex rounded"). Tucker (1983) likewise absorbed the full range of observations into a single description ("scales … ovate-obovate … acute to obtuse … light brown to reddish brown"). The variation observed within Bentham's flatsedge is continuous and compounded by artifacts of preservation and methodology; it does not approach the level required for species delimitation.

Number of stamens.—Chermezon (1919), among other proposed diagnostic characteristics (Fig. 4), cited stamen number as a distinguishing character, attributing 3 stamens to *P. albomarginatus* and 2 to *P. tremulus*. Previous treatments described both *C. tremulus* and *C. albomarginatus* with variably 2–3 stamens (Steudel 1855; Clarke 1886), and modern regional treatments report the same for specimens from Central America and East Africa (Tucker 1983; Hoenselaar et al. 2010). Even Kükenthal (1935–1936), who described *C. albomarginatus* with "Stamina 2 vel 3" and *C. tremulus* "Stamina 2," contradicted his own delimitation by treating *C. colchicus* and *C. stachyphorus* as varieties of *C. tremulus*—the protologues for both describe them as possessing "Stamina 3" (Koch 1848). This infraspecific variation in stamen number has also been observed in our own material from Arkansas, Missouri, and Mississippi; this character cannot serve as a basis for species-level separation within Bentham's flatsedge.

The characters addressed above—habit, glume morphology, and stamen number—are variable but



P. albomarginatus.	*P. tremulus.*
Anthèle d'ordinaire peu étalée.	Anthèle très étalée et généralement plus fournie.
Epillets jaunâtres, larges (3-4 mm.).	Epillets d'ordinaire d'un brun plus ou moins rougeâtre, plus étroits (2-2 1/2 mm.).
Trois étamines.	Deux étamines.
Akène mûr obovoïde, noir, gros (2 mm. sur 1 1/4-1 1/2).	Akène mûr oblong, brun, plus petit (1 1/2 mm. sur 3/4).

Fig. 4. The diagnostic suite of characters described by Chermezon (1919) for differentiating *P. albomarginatus* and *P. tremulus.*

uncomplicated: each can be shown to vary within Bentham's flatsedge without requiring a mechanistic explanation for how or why. The remaining characters are not so simple. Inflorescence ramification has been treated as distinctive by multiple authorities, but its variation is governed by environmental conditions during development. Achene shape, achene color, and spikelet width are three expressions of a single developmental sequence, and disentangling that sequence reveals that the morphological spectrum observed within Bentham's flatsedge does not warrant its separation into two species.

Inflorescence ramification.—A commonly cited distinction between the two putative species is the complexity of the inflorescence: strictly compound (i.e., primary rays bearing secondary rays but no further branching; maximum ramification reaching second-order paracladia) in *C. colchicus* and *C. albomarginatus*; compound to decompound (i.e., secondary rays themselves sometimes branched, producing third-order paracladia) in *C. stachyphorus* and *C. tremulus* (Koch 1848; Clarke 1886; Chermezon 1919; Kükenthal 1935–1936). However, inflorescence ramification is known to be environmentally plastic, and its unreliability for species delimitation in *Cyperus* s.l. has been recognized for well over a century—C.B. Clarke (1886) himself observed that "the degree of the development of the umbel would therefore be a character of little [taxonomic] value …" within this genus.

Raynal (1971), for example, argued that in species capable of producing higher-order branching, the degree of inflorescence ramification is driven primarily by the nutritional conditions prevailing during inflorescence initiation—vigorous, well-resourced plants simply branch more. He observed this directly with *C. congensis* C.B. Clarke in Senegal, where the same population produced two distinct inflorescence forms over the course of a single year: plants whose inflorescences were initiated during the dry season but opened at the onset of flooding bore poorly divided rays with elongated spikelets, while those produced later under more typical conditions bore well-divided rays with shorter spikelets. On this basis, Raynal concluded that the degree of ramification of the anthelodium varies considerably as a function of site conditions, and that the taxonomic varieties historically erected on differences in branching complexity—"*simplex*," "*subdecompositus*," and the like—were founded on what was, in reality, intraspecific, environmentally induced variation.

Later work across Cyperaceae has confirmed that this plasticity is not unique to *C. congensis*: Vegetti (2003) documented wide variation in the degree of paracladial development within and across genera, and Guarise and Vegetti (2008), studying *Cyperus* sect. *Luzuloidei,* noted that inflorescence form in *C. entrerianus* Boeck. is "considerably influenced by the environmental conditions," with the same species producing compound anthelodia under favorable conditions and simple or capitate inflorescences under unfavorable ones. Similar observations have been made for Bentham's flatsedge: Blatter and McCann (1934) explicitly note "Umbels generally very large but we have seen specimens with the inflorescence reduced to a few spikes." Our

own field observations in rice fields of Arkansas and Missouri and drawdown mudflats in Mississippi are fully consistent with these findings: the full spectrum of inflorescence complexity in Bentham's flatsedge—from compact, few-rayed compound anthelodia on stressed or late-season individuals to fully decompound, many-rayed anthelodia on vigorous plants at peak growing season—can occur within populations separated by no more than a few meters, and sometimes within the synflorescence of a single individual. Inflorescence ramification, in short, is not a reliable character for species delimitation in this complex.

Achene dimensions, achene color, and spikelet width.—These three characters have been cited together in every major treatment from Clarke (1886) to Haines and Lye (1983) as evidence for the separation of *albomarginatus* (broadly obovate, black achenes in wider spikelets) from *tremulus* (more oblong, brown achenes in narrower spikelets). In fact, all three are products of the same developmental sequence, and understanding that sequence dissolves all three characters simultaneously.

In our material from Arkansas, Missouri, and Mississippi, plants grown from seed in the greenhouse, and the extensive herbarium collections examined for this work, achene development in Bentham's flatsedge appears to follow a two-phase process. We present this process here as a working model based on direct observation rather than formal characterization, offered as a framework consistent with both our material and the historical descriptions discussed below; a dedicated developmental study would be a valuable follow-up. In the first phase—filling—the fertilized ovary swells as the achene accumulates reserves, expanding to the maximum size permitted by available resources. Throughout this filling phase, the achene has not yet begun to darken, remaining unpigmented (appearing white to cream-colored) regardless of its eventual size. Achene shape at the end of this phase is a function of the resources the plant was able to allocate: achenes receiving adequate resources fill to their genetic potential and assume a broadly obovate form, while achenes developing under stress—late in the season, on a nutrient-poor site, or on a plant whose spikelet production outpaced its eventual resource budget—remain narrower and more oblong. As the achene swells, it pushes its subtending glume away from the rachilla—producing, at the spikelet level, the characteristic non-overlapping glume arrangement that is diagnostic for this species at maturity. The degree of glume spread is directly proportional to the degree of achene fill: plump achenes spread the glumes widely, producing a wider spikelet, while poorly filled achenes leave them closer together, producing a narrow one—this can most easily be seen among variably matured inflorescences within the synflorescence of an individual with multiple culms (Fig. 5). Spikelet width, in other words, is not an independent character at all—it is a direct physical consequence of how completely the achenes have filled. When Chermezon (1919) reported narrower spikelets and narrower achenes in *P. tremulus* relative to *P. albomarginatus* (Fig. 4), he unknowingly documented a symptom of this very phenomenon. The correlation is not coincidental; it is causal.

Once filling is complete and the achene has reached its final dimensions, the second phase—maturation—begins. The pericarp hardens and darkens, with pigmentation proceeding basipetally from the style base (the distal pole of the achene) toward the rachilla (the proximal pole), advancing in a visible wave from cream-white through brown, castaneous, and finally jet black. If caught at the right stage, the achene can display a bicolored appearance—dark at the apex, pale at the base—that reflects the advancing front of pericarp maturation (Fig. 6). The critical point is that these two phases are generally sequential, not simultaneous; an achene will typically finish filling before it begins to mature. A large, well-filled achene that has only recently entered the maturation phase may be broadly obovate but still pale brown; a small, poorly filled achene that has had ample time to mature may be narrowly oblong but fully black. An achene's position on the spectrum from broadly obovate to narrowly oblong reflects the outcome of the filling phase, while color indicates progress through the maturation phase. The two characters can co-vary—a stressed, late-season plant may produce achenes both narrow and pale brown—but are frequently independent of one another. The developmental sequence described here was observed directly in our material and in greenhouse-grown plants; its consistency with historical descriptions and presence of associated features in herbarium specimens collected from across the species' range suggests it is characteristic of the species as a whole rather than a regional phenomenon.

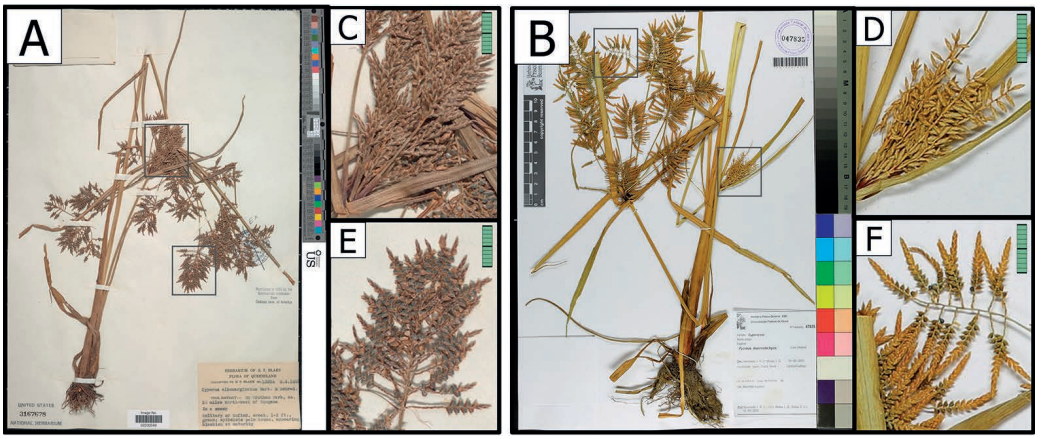


Fig. 5. Examples of within-synflorescence variation in maturity. A. From Australia, *S.T. Blake #13694,* [US:3167678]. **B.** From Brazil, *L.R.O. Normando et al. #327,* [EAC0047834]. **C.** & **D.** Immature inflorescence with spikelets appearing narrower (scale = 1 cm). **E.** & **F.** Further-matured inflorescence with achenes filled, spreading their subtending glumes widely; spikelets appearing wider (scale = 1 cm).



Fig. 6. Achenes of *Cyperus flavicomus* Michx. at different stages of fill and maturity, all taken from a single individual collected at Grenada Lake, Mississippi, U.S.A., 18 October 2025 (*A.D. Ross & C.T. Bryson #s.n.*, [AWS-2025-GREN]). Some portray the "bicolored" appearance discussed in the text. Photo: A.D. Ross.

This dissociation is visible across various historical descriptions of Bentham's flatsedge. If achene shape and color were expressions of a single underlying variable—whether taxonomic or developmental—then broadly obovate achenes should always be darker, and narrowly oblong achenes always paler. Indeed, Steudel (1855) described the achenes of *C. albomarginatus* as "obovato … nigro" and of *C. tremulus* as "obovato-oblongo … laete castaneo nitidulo"—the former broadly obovate and black, the latter more oblong and light brown. Chermezon (1919) records the same (Fig. 4): "Akène mûr obovoïde, noir, gros" for *P. albomarginatus,* "Akène mûr oblong, brun, plus petit" for *P. tremulus*; these descriptions suggest that shape and color co-vary, and one might reasonably interpret the difference as taxonomically informative.

However, other descriptions illustrate that the two characters are wholly independent of one another: Small (1913) described *C. hochstetteri* with "achenes lenticular, obliquely obovoid-orbicular … deep brown"—broader than that of C. flavicomus (by their description "achenes obovoid, lenticular, black"), yet not as dark—a well-filled achene that had not yet finished maturing at the time of collection and examination. Conversely, Kükenthal (1935–1936) described *C. tremulus* with "Nux … obovato-oblonga … spadicea demum nigra"—narrower than that of *C. albomarginatus* ("Nux … obovata"), yet still darkening to black; his "demum nigra"—eventually black—concedes that even the more oblong achenes reach the same terminal color given sufficient time. All four combinations of shape and color—broad and black, broad and brown, narrow and black, narrow and brown—are represented in the literature, drawn from specimens collected at different times, in different conditions, at different stages of development. These are not descriptions of two species, but of one.



Fig. 7. Examples of spikelets showcasing a visible maturation gradient in key specimens of *Cyperus flavicomus* Michx. (scale = 1 cm). A. Lectotype of *Cyperus hochstetteri* Nees ex Krauss (*Kotschy #52,* [TUB-007269]). **B.** Paralectotype of *Cyperus ornatissimus* F. Muell. (*F. Mueller #s.n.,* [K000881556]). **C.** Lectotype of *Cyperus patuliflorus* Boeck. (*J. Stocks #s.n.,* [K000592585]).

The developmental gradient within a single spikelet provides the clearest demonstration (Fig. 7) that all three characters—achene dimensions, achene color, and spikelet width—are expressions of a single developmental sequence. Spikelets of *Cyperus* are indeterminate: flowers and their subtending glumes are initiated acropetally along the rachilla, with proximal flowers developing first and distal ones last (Vrijdaghs et al. 2010). As the first to be initiated, the proximal flowers are the first to reach anthesis, the first to be fertilized, the first to enter the filling phase, and the first to progress into the maturation phase (cf. Blatter & McCann 1934). The practical consequence—noted in passing by Kees et al. (2025), who remarked that "because of the indeterminate growth of spikelets, florets can usually be found near the spikelet apex"—is that a spikelet seen before complete maturation can display a base-to-apex gradient in all three characters simultaneously: proximal achenes fully filled, jet black, and pushing their subtending glumes widely apart; middle achenes fully filled but still pale brown or castaneous with moderately spread glumes; and distal achenes still in the filling phase—white, undersized, with glumes still imbricate.

In Bentham's flatsedge, this gradient is made visually conspicuous by the species' diagnostic non-overlapping glume arrangement. The glumes begin fully imbricated when immature and progressively spread apart as their associated achenes swell and push them open (Fig. 7). The range of glume spread within a single spikelet—tight at the apex, wide at the base—is a reliable field indicator of where each achene sits in the developmental sequence, and it is this variation that previous taxonomists unwittingly partitioned into species: specimens collected early in the fruiting season, or from stressed plants that never attained their full genetic potential, yielded the narrow, brown-achened, narrow-spikeleted form attributed to *C. tremulus,* while specimens collected at full maturity yielded the plump, black-achened, wide-spikeleted form attributed to *C. albomarginatus.*

The earliest record of this gradient in Bentham's flatsedge may be from Elliott (1821), who observed of *C. flavicomus* Michx. that "the umbels exhibit generally a yellowish hue, but many of the spikes are tinged near the base with a dull leaden color." This "dull leaden color" near the base of each spike is the darkened pericarp of the earliest-maturing proximal achenes visible through the thin glumes, grading into the paler hue of the still-developing achenes above. This is precisely the pattern expected from acropetal flower initiation: the proximal achenes, having been fertilized first, are the first to complete both phases of development, and their darkened pericarps become visible while more distal achenes continue to develop. Blatter and McCann (1934) recognized this as a general phenomenon in *Cyperus,* noting that "the colour varies considerably with the age of the nut."

Haines and Lye (1983) came closest to recognizing the morphological implications of this developmental sequence. In their description of *C. macrostachyos* ssp. *tremulus,* they wrote: "Nutlet … oblong, apiculate, light brown with minute papillae in longitudinal rows (only immature nutlets seen in Ugandan specimens), but mature nutlets probably larger and with darker color." This is a direct acknowledgment that they believed the

lighter color and narrower shape of the tremulus achenes in their material to be an artifact of collection timing—not a fixed taxonomic character—and that they expected fully mature achenes to converge on the form described for *C. macrostachyos* ssp. *macrostachyos*: "Nutlet … obovate to oblong, grey, dark brown or blackish; apex strongly or slightly apiculate; surface with minute papillae in distinct longitudinal rows." The two subspecific descriptions, ostensibly of different taxa, describe a single achene at two stages of development. The only difference between them is time and environment.

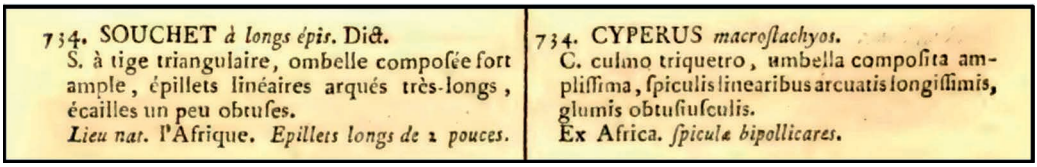
In summary, none of the characters historically employed to separate Bentham's flatsedge into two species withstands scrutiny. Every purported diagnostic difference is either environmentally plastic, maturity-dependent, or both, and the variation across the range of the species is continuous—fully consistent with a single, widely distributed, phenotypically variable taxon. Having established that the morphological variation within Bentham's flatsedge does not support its division into two species, we turn to the nomenclatural history of the names applied to it—beginning with *C. macrostachyos* Lam.

Concerning C. macrostachyos.—The modern application of *C. macrostachyos* Lam. to Bentham's flatsedge can be traced ideologically to the initial treatment of Hooper and Raynal (1969), who published the comb. nov. *Pycreus macrostachyos* (Lam.) J. Raynal as the "correct" name for *P. albomarginatus* (Mart. & Schrad. ex Nees), calling *macrostachyos* an "overlooked epithet" for the well-known species. Unbeknownst to Hooper and Raynal, *macrostachyos* had not been "overlooked"—it would be more accurate to say that the name *C. macrostachyos* Lam. had been abandoned.

The anomalous protologue.—A systematic examination of Lamarck's *Cyperus* entries in the Tableau Encyclopédique (1791), undertaken for the present study, reveals a highly consistent citation pattern not previously documented in the literature. When Lamarck described species he considered new to science, he almost invariably cited the collector who furnished the material, and frequently cited a published illustration or earlier description in support: e.g., *C. pennatus* Lam. (#703: "Ex Java. Commerç."), *C. compactus* Lam. (#706: "E Madagascaria. Commerç."), *C. strictus* Lam. (#721: "Ex Java. Commerç."), *C. malaccensis* Lam. (#725: "Ex Malacca. Sonner. An. Cyp. n°. 52. Rottb. Exclus. synonymis"), *C. laxus* Lam. (#730: "E Cayenna, Brasilia. Sloan. hist. 1. t. 75. f. 1."), *C. prolifer* Lam. (#733: "Ex insula Franciæ. Jos. Martin."), and *C. polycephalus* Lam. (#738: "E Cayenna. D. Stoupy. Rottb. t. 13. f. 2."). Even when locality data were absent, Lamarck still credited the collector—as in *C. juncoides* Lam. (#735) and *C. spadiceus* Lam. (#736), where dots occupy the locality field ("..... Sonnerat."), indicating that Lamarck received the specimen without geographic data but still acknowledged Sonnerat as its source.

For already-published names, in contrast, Lamarck typically gave only a broad geographic label with no collector attribution, and occasionally a citation of the earlier description: e.g., *C. fascicularis* Poir. (#708: "T. 38. f. 2," "E Barbaria. D. Poiret."), *C. longus* L. (#711: "E Gallia, Italia, Hispania."), *C. esculentus* L. (#712: "L. Ex Italia, Oriente."), *C. squarrosus* L. (#714: "L. Ex Asia."), *C. haspan* L. (#728: "Lin. Ex India, Æthiopia."), and *C. papyrus* L. (#732: "Ex Ægypto, Madagascaria."). Perhaps for such universally recognized species, Lamarck felt no obligation to cite either the original publication or a collector.

The protologue of *C. macrostachyos* (#734), of those examined, is the only one that breaks this pattern. It reads: "C. culmo triquetro, umbella composita amplissima, spiculis linearibus arcuatis longissimis, glumis obtusiusculis. Ex Africa. Spicula bipollicares" (Fig. 8). There is no collector, no literature reference, and no herbarium annotation—only the vague "Ex Africa" locality and a morphological note recording the spikelets as "bipollicares" (≈ 5 cm long). This citation style is indistinguishable from that of Lamarck's re-treatments of Linnaean species, yet no earlier published descriptions exist for which *C. macrostachyos* could be a re-treatment; the major pre-1791 sources for illustrations of Cyperaceae—Rottbøll (1773) from India, Arabia, and the Cape; Sloane (1707–1725) from the Caribbean; Plukenet (1700) from the East and West Indies; Burman (1768) from India; and Forsskål (1775) from Egypt and Arabia—contain nothing matching the description of Lamarck's large-spikeleted "Ex Africa" *C. macrostachyos*. The entry is the only new *Cyperus* species in this work that lacks both a collector citation and a bibliographic reference. The protologue is thus best explained as Lamarck describing material of uncertain provenance—most likely a specimen bearing


734. SOUCHET *à longs épis.* Dict.
S. à tige triangulaire, ombelle composée fort ample, épillets linéaires arqués très-longs, écailles un peu obtuses.
Lieu nat. l'Afrique. *Epillets longs de* 2 *pouces.*

734. CYPERUS *macrostachyos.*
C. culmo triquetro, umbella composita ampliſſima, ſpiculis linearibus arcuatis longiſſimis, glumis obtuſiuſculis.
Ex Africa. *ſpiculæ bipollicares.*

Fig. 8. The full protologue of *C. macrostachyos* Lam. (1791).

only a vague "Africa" label and no collector name—though the specific measurement "spicula bipollicares" confirms that he worked from a physical specimen rather than a published illustration. Whatever its source, the material reached Lamarck without the accountability or bibliographic support that accompanied every other new species he published in the same treatment.

Fragmentary material.—Lamarck's original material can be found today preserved in two sheets at P ([P00668535]; [P00573081]), both of which are merely partial inflorescences (Fig. 9). This deficiency appears to be original, not the result of subsequent damage. A contemporary label accompanying the smaller specimen ([P00573081]) identifies the mounted material as "*Cyperus macrostachyos*—Lam. faible portion de la panicule" and places it in Poiret's herbarium—the material is, by its own label, a small fragment of the original. This is consistent with Poiret's (1806) own published account; having examined the material in Lamarck's herbarium, he explicitly noted: "La partie supérieure de cette belle plante, la seule portion que j'aie vue, …"—the upper portion of the plant was all he saw. The specimen sent by Lamarck to Vahl for his 1805 work was likewise only fragmentary, as reported by Kunth (1837): "Vahl. Enum. 2. 349 et herb. (suppetit frustulum [radius] a Lamarckio cum Vahlio communicatum.)." The original material was fragmentary when Poiret examined it and took a portion for his own collection (as he often did, cf. *C. tremulus*: *L.M.A. du Petit-Thouars #s.n.* in App. 2; *C. malaccensis* and *C. latifolius* in App. 3), fragmentary when Lamarck sent it to Vahl, and fragmentary when Kunth reported on it. No morphologically complete specimen of *C. macrostachyos* Lam. has ever been known to exist.

In their recent work, Pereira-Silva et al. (2022) presumed that the holotype must be a morphologically complete specimen. Unable to locate any complete specimen and finding only the partial material on [P00668535], Pereira-Silva et al. noted that "… there is no evidence that Hooper and Raynal (1969) have seen a sheet bearing a morphologically complete specimen, …" and concluded that the true holotype must have been lost. Hence, they assumed that Hooper and Raynal (1969) had mistakenly applied the term "holotype" to what was in fact a surviving fragment, and redesignated it as a lectotype. But the holotype was never lost—it was simply never complete.

Raynal, who was Deputy Director of the Laboratory of Phanerogamy at the Muséum national d'histoire naturelle where Lamarck's herbarium is maintained, had personally examined the smaller specimen [P00573081] prior to his 1969 publication—his own determination slip, dated 1 December 1968, is still affixed to it. That same sheet bears the annotation "holotype in herb. Lamarck," directing the reader to the larger specimen [P00668535], which in turn bears the notation "ex herb. D. La Mark," confirming its provenance from Lamarck's collection. The labels on the two sheets, read together, are internally consistent and unambiguous: [P00668535] is the holotype, and [P00573081] is a fragment removed from it for Poiret's collection in Aisne (approximately 150 km north of Paris), subsequently passing through the herbaria of Moquin-Tandon and Cosson before being eventually incorporated into the general collections at P—not an independent duplicate. Both sheets carry museum-applied "ISOTYPE" stamps (Fig. 9), but these contradict the sheets' own annotations and are here regarded as cataloguing errors.

Hooper and Raynal's (1969) citation of this material as the holotype was correct, although the reinterpretation of Pereira-Silva et al. (2022) was well within reason. We treat [P00668535] as the holotype and

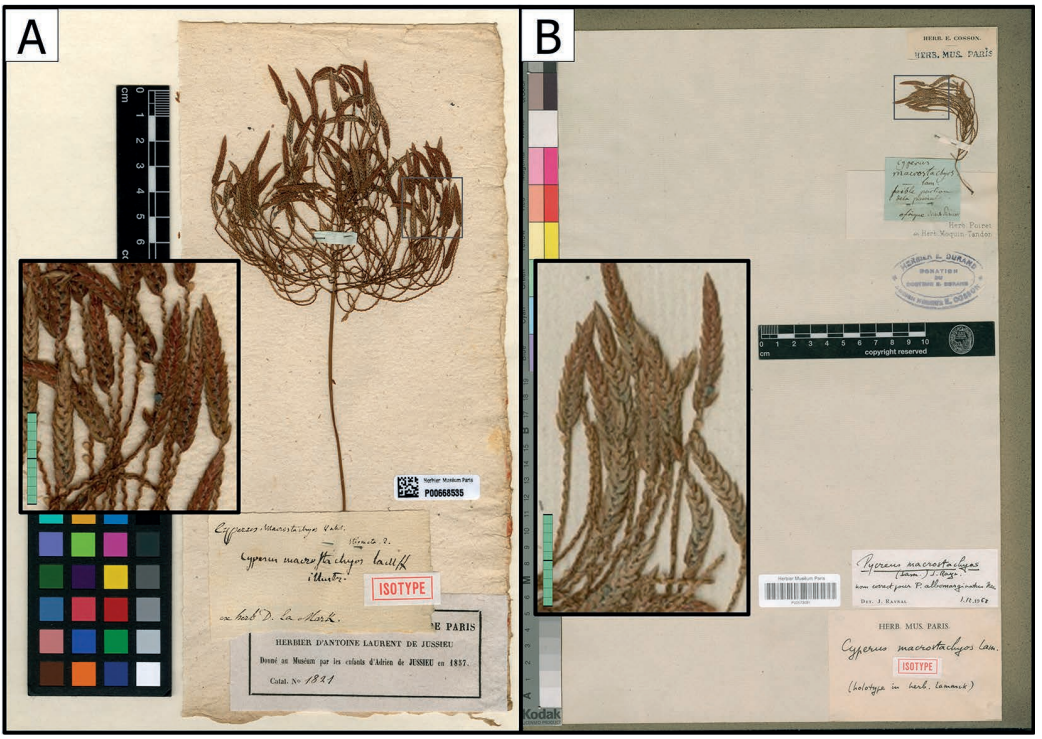


Fig. 9. Lamarck's original material for *Cyperus macrostachyos* Lam. A. Holotype (*s.c. #s.n.,* [P00668535]) and zoomed-in inflorescence of holotype (scale = 1 cm). B. Holotype fragment (*s.c. #s.n.,* [P00573081]) and zoomed-in inflorescence of holotype fragment (scale = 1 cm).

[P00573081] as a holotype fragment. From its first description to the present day, the taxon has been known only from fragmentary, upper-inflorescence material insufficient for adequate diagnostic description.

Vahl's description.—Recognizing the inadequacy of Lamarck's protologue, Vahl (1805) expanded the concept of *C. macrostachyos* by combining Lamarck's African fragment with a morphologically complete *Cyperus* s.l. specimen from India (collected by Rottler), which he took to be a member of the same species. It was Vahl's more detailed description of *C. macrostachyos*—not Lamarck's—that subsequent workers largely used for diagnoses of the taxon. The Rottler specimen, though not located during the present study, was consistently identified by subsequent authors—including Kunth (1837), C.B. Clarke (1886,1894), and Kükenthal (1935–1936)—as belonging to the Indian species *C. puncticulatus* Vahl, which Vahl had initially distinguished from *C. macrostachyos* primarily on the basis of the latter's unusually elongated spikelets; a character now understood to reflect environmental variation rather than taxonomic distinction, and a natural extension of the aforementioned effect of environment on inflorescence ramification (Raynal 1971; C.T. Bryson, pers. comm.).

Progressive doubt of "Ex Africa" locality.—Subsequent authorities, primarily trusting Vahl's expanded description, progressively distanced themselves from the African provenance. Lamarck's "Ex Africa" locality was last confidently cited by Roemer and Schultes (1817); A. Dietrich (1833), in his continuation of Willdenow's Species Plantarum, omitted the African locality entirely, giving only Rottler's Indian locality—and D.N.F. Dietrich (1839) maintained that omission in his own later work. The most telling intervention, however, was that of Kunth (1837), who marked the African provenance with an explicit question mark ("? Africa") and first treated *C. macrostachyos* as a subspecies of *C. puncticulatus*—acknowledging morphological identity while

flagging the locality as unreliable. Within approximately forty years of Lamarck's original publication, no author could corroborate an African origin for the specimen.

The severance of macrostachyos from puncticulatus.—Despite the consensus that *C. macrostachyos* was morphologically referable to *C. puncticulatus,* the unresolved "Ex Africa" provenance prevented its formal incorporation into the synonymy of a species considered endemic to South Asia. The name eventually fell out of active use entirely, owing in large part to an error by Steudel (1841). Steudel placed *C. macrostachyos* as a synonym of *C. puncticulatus* at the entry for *macrostachyos* on page 470, but erroneously omitted it from the listed synonymy under *puncticulatus* on page 472 (Fig. 10). This error was upheld in his later Synopsis Plantarum Glumacearum (1855), effectively severing the link between the two names for any worker consulting only the puncticulatus entry.

C.B. Clarke (1886; 1894), working from Kunth's 1837 treatment and with access to Vahl's herbarium material, recognized *C. macrostachyos* Vahl as a synonym of *C. puncticulatus,* but explicitly excluded Lamarck's original material from his synonymy entirely ("as to plant of Rottler, not of Lamarck [P00668535] or Poiret [P00573081]"). Kükenthal (1935–1936) went further, again treating *C. macrostachyos* Vahl under *C. puncticulatus* while placing *C. macrostachyos* Lam. among "Species incertae sedis vel inextricabiles"—species of uncertain or indeterminable placement. Essentially, post-Lamarck authors ultimately agreed on the morphological identity, but could not reconcile it with its stated African provenance, and the name was left unplaced.

The treatment of Hooper and Raynal.—The history of the name *C. macrostachyos* presents a nomenclatural reality that Hooper and Raynal did not account for. *C. macrostachyos* Vahl—the expanded concept including Rottler's Indian material—had been treated as a synonym of *C. puncticulatus* by every major cyperological authority for well over a century (Kunth 1837; Clarke 1886; Clarke 1894; Kükenthal 1935–1936). Had Hooper and Raynal (1969) encountered this established synonymy, they would have been compelled to specify "non Vahl" in their basionym citation to distinguish their interpretation of Lamarck's original material from Vahl's later concept. The absence of any such specification in their work demonstrates that they were unaware of the entire post-Lamarck history of the name—they did not know that *C. macrostachyos* had been absorbed into *C. puncticulatus*, much less that it had been essentially abandoned.

Because of this, they would have had no reason to question the "Ex Africa" label on the holotype of *C. macrostachyos* Lam. Evidently, Raynal saw a specimen belonging to *Pycreus* labeled "Ex Africa" with whitish-hyaline glume margins, and understandably mistook it for the only widespread African taxon matching the description: *P. albomarginatus.* Conceptually, this was a very strong argument—strong enough, apparently, that Hooper and Raynal did not consider it necessary to actually examine the types of *P. albomarginatus, C. tremulus,* or any of the names circumscribed within their *P. macrostachyos,* to confirm conspecificity (Hooper & Raynal 1969; Hooper 1972; Tucker 1985).

The application of *P. macrostachyos* sensu Hooper and Raynal to Bentham's flatsedge—now *C. macrostachyos* following the decision of Larridon et al. (2014) to reintegrate *Pycreus* into *Cyperus* s.l.—has become entrenched in modern taxonomic and floristic works, but this has been the perpetuation of an assumption, never once actually verified (Tucker 1985; cf. Hooper & Raynal 1969; Hooper 1972; Hoenselaar et al. 2010; Pereira-Silva et al. 2022; Mesterházy et al. 2022). In fact, the only author documented to have personally examined the types of both *C. macrostachyos* and *C. albomarginatus* reached the opposite conclusion.

When Tucker (1985) personally examined the types of *C. flavicomus, P. albomarginatus,* and *C. macrostachyos*—remarkably, the first author to document examination of the *C. flavicomus* holotype since Michaux himself—he explicitly rejected the treatment of Hooper and Raynal (1969). Tucker described the *C. macrostachyos* type as "strikingly different from *C. flavicomus* Michx. (= *C. albomarginatus*), notably in its long spikelets with 60 to 70 closely imbricate scales," concluding that "the type of *C. macrostachyos* Lam. clearly does not belong in the same species as *C. flavicomus.*" He identified the material instead with *C. puncticulatus* var. *quinquagintiflorus* C.B. Clarke sensu Kükenthal (1935–1936), citing Kunth (1837) in support. Tucker asserted that the then-forgotten *C. flavicomus* Michx. was the correct name for *C. albomarginatus,* the name widely applied to North American collections of Bentham's flatsedge since the treatments of Clarke (1886)

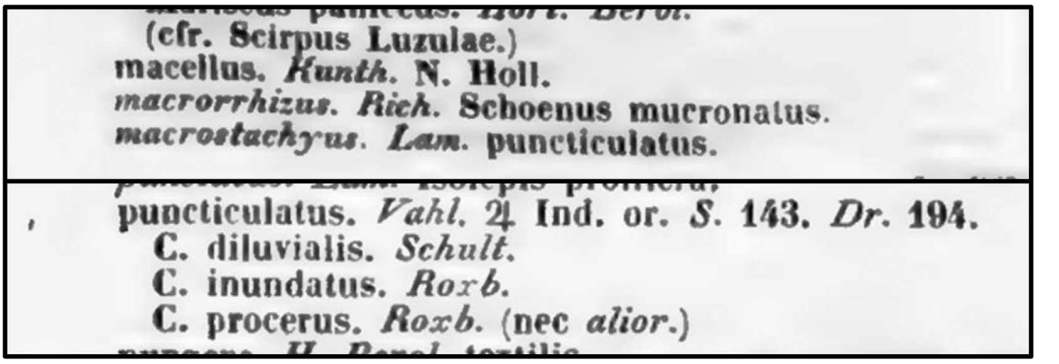


Fig. 10. Steudel's (1841) erroneous omission. Top: entry for *Cyperus macrostachyos* Lam. clearly designating the name as a synonym of *Cyperus puncticulatus* Vahl (p. 470). Bottom: entry for *Cyperus puncticulatus* Vahl, without *"macrostachyus"* listed as a synonym (p. 472).

and Kükenthal (1935–1936). He did not, however, address *C. tremulus,* which had already been synonymized with *P. albomarginatus* by Wild and McEwen (1961), and under *C. macrostachyos* by Hooper (1972). This left the disposition of the *tremulus* element of Bentham's flatsedge entirely unresolved: a subsequent author could reasonably have retained it under *C. macrostachyos* sensu Hooper (1972), transferred it to *C. flavicomus* sensu Tucker (1985), or re-elevated it to species rank.

Because Tucker (1985) published his findings in Rhodora, a journal with primarily North American readership, his conclusions went largely unnoticed outside North America. This is the origin of the modern nomenclatural split: *C. flavicomus* in North America, *C. macrostachyos* elsewhere. The history of *C. flavicomus* Michx. is nomenclaturally simpler but no less consequential.

Concerning C. flavicomus.—*Cyperus flavicomus* was first described by André Michaux (1803) in Volume I of his Flora Boreali-Americana. In full, the protologue reads "FLAVICOMUS. C. majusculus, basi foliosus; involucro longissimo, reflexo : umbella composita; ramulis ab ipsa basi floridis; spicilis patentibus, flavis, oblongis, 7-floris. OBS. Culmus triqueter : involucrum sub5-phyllum : umbella confertiuscula; umbellulae secundariae ex. ramulis simplicibus, ab ipsa basi spicatim spicilliferis : spiculae squamis obtusis, margine scariosis. HAB. in Carolina."

Holotype sheet confusion.—The sheet bearing the holotype of *C. flavicomus* Michx., housed at P ([P00667331]), carries two distinct specimens. On the right, a large plant clearly labeled "*Cyperus flavicomus*; Hab. in Carolina"—this is the true holotype (Fig. 11: A, B). On the left, a much smaller specimen inconspicuously labeled "*Carex*? cor. nulla calix palei distichis, stam. tria, styli 3, semen unicum nudum: ad ripas Sioto & Ohio" [with "*Carex*?" struck through] (Fig. 11: E, F). Several lines of evidence confirm that the smaller specimen on this sheet has no bearing on the typification of *C. flavicomus*.

First, Michaux describes the spikelets of his *C. flavicomus* as "7-floris." The spikelets on the large specimen are indeed 7-flowered, while those of the small specimen bear approximately 8–12 florets per spikelet (Fig. 11: C, D, G). Second, the stated locality of the small specimen—"ad ripas Sioto & Ohio"—corresponds to the confluence of the Scioto and Ohio rivers near Portsmouth, Ohio, U.S.A. (cf. Henry 2004), approximately 250 km north of the historical boundaries of the Carolinas. When Michaux cites material "Hab. in Carolina" in the protologue of *C. flavicomus,* he could not have intended the inclusion of this smaller specimen. Third, and decisively, the annotation on the small specimen notes "styli 3." A trifid style categorically excludes placement in *Pycreus,* where styles are invariably bifid. Based on the trifid style, the presence of 3–4 distinct lateral nerves on each side of the glume extending nearly to the margin, and the membranous uncolored glume margin, the small specimen appears more consistent with *C. esculentus* L.; regardless, it belongs to *Cyperus* s.s. and has no relevance to the application of the name *C. flavicomus* Michx.

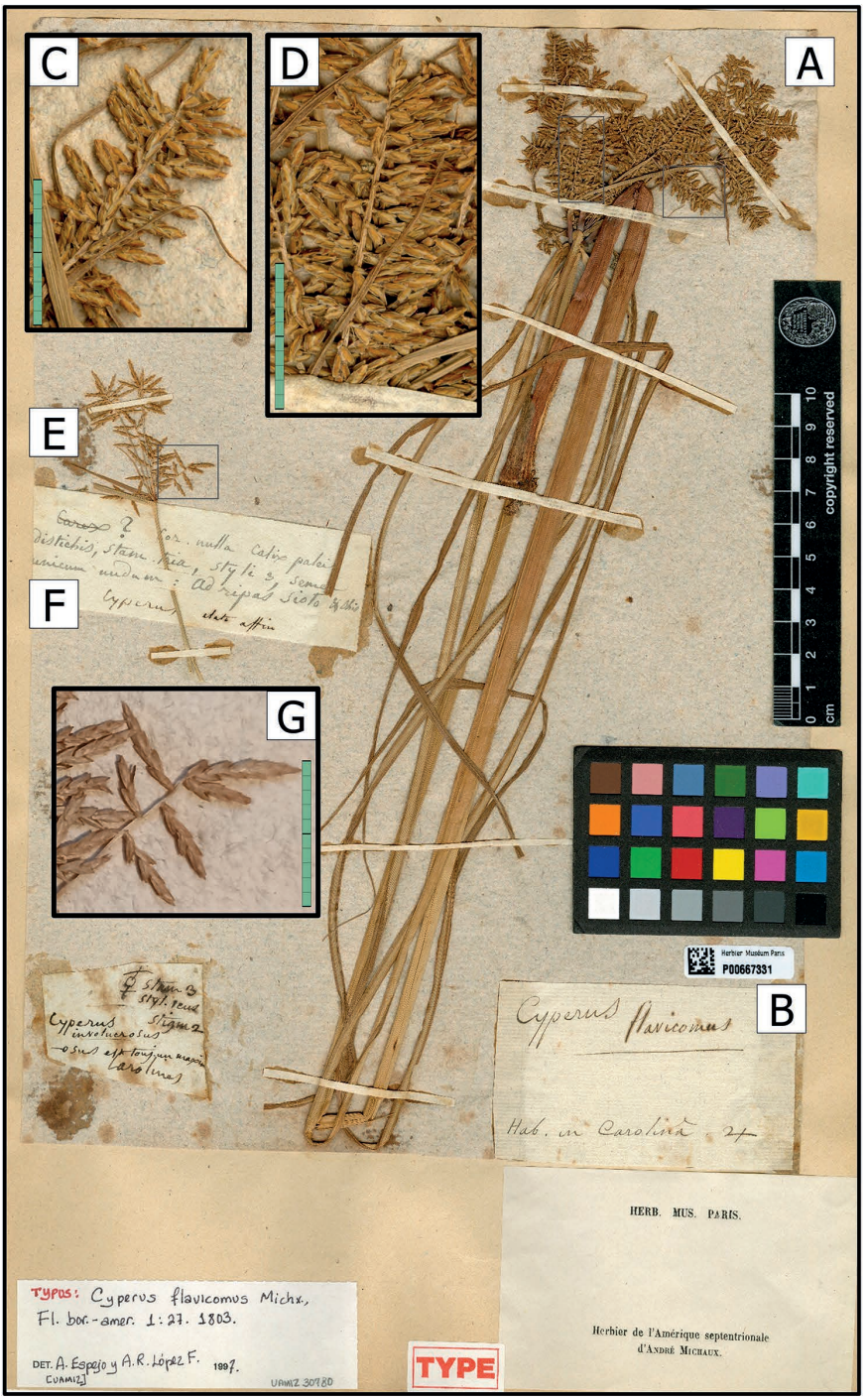


Fig. 11. **The holotype-bearing sheet of *Cyperus flavicomus* Michx. A. & B. The true holotype of *Cyperus flavicomus* Michx. (*Michaux #s.n.*, [P00667331]) and accompanying note *"Cyperus flavicomus,"* "Hab. in Carolina ♃." C. & D. Zoomed-in inflorescence of the *Cyperus flavicomus* Michx. holotype (scale = 1 cm). E. & F. *Cyperus* sp. (cf. *Cyperus esculentus* L.) and accompanying note "Carex? cor. nulla calix palei distichis, stam. tria, styli 3, semen unicum nudum: ad ripas Sioto & Ohio." G. Zoomed-in inflorescence of *Cyperus* sp. (scale = 1 cm). Photos: Full sheet (A–F): © MNHN – J. Mainguy; G: C. Aupic.**

The only apparent consequence of this holotype sheet confusion was that Vahl, when preparing his own description of *C. flavicomus,* worked from mixed material—a fact noted by C.B. Clarke (1886), who observed "*C. flavicomus* Vahl, partim e *C. strigoso,* partim e *C. flavicomo* nostro, descriptus est." Some of Vahl's examined non-*flavicomus* material can be seen today on a sheet held at MPU ([MPU028131], Fig. 12; cf. *C. filicinus* Vahl) bearing two plants collected by L.A.G. Bosc from South Carolina, annotated (Fig. 12: D) "dans l'herbier de Michaux au *C. flavicomus* il y a un petit rameau de panicule de celui-ci—et un grand échantillon d'un autre qui est fort distinct," confirming that the mixed composition of Michaux's sheet was recognized early; as well as the later note (Fig. 12: E) "ne concorde pas très bien avec la description—Kunth Enumer. pl. p. 15. №. 37," further confirming that the mounted plants were recognized as inconsistent with *C. flavicomus* as circumscribed by Kunth (1837). Several loose achenes of Bentham's flatsedge on this otherwise non-*flavicomus* sheet corroborate that Vahl examined the mixed material simultaneously (Fig. 12: C). The true *flavicomus* material described by Vahl (1805) can be found today at C (fide Tucker 1985).

Overall, the species was well-received in early North American botanical literature and was applied without controversy by subsequent authors. By the 1870s, several authors had begun to note the similarity of *C. flavicomus* with African concepts such as *C. tremulus* (Baker 1877; Boissier 1884), a relationship formally recognized by Boeckeler (1868) and Bentham and Mueller (1878).

Clarke's crucial misstep.—Around this time, C.B. Clarke encountered a misidentified specimen of *C. strigosus* L. held at LINN ([LINN-HS 104.21]), labeled "*flavicomus* Pursh 53, n. 19"—to this day still stored under the name *C. flavicomus* (Fig. 13). Based on this specimen alone, Clarke (1886) asserted that "*C. flavicomus,* Mich. Fl. Bor.-Am. i. p. 27, 'spiculis 7-floris' (Pursh. Fl. i. p. 53), est *C. strigosus,* Linn."; Clarke had clearly not seen Michaux's holotype, which is readily distinguishable. Nevertheless, Clarke's treatment proved immediately influential; contemporary authors began citing Vahl as the authority for *C. flavicomus* rather than Michaux (cf. Britton 1886; Engler & Prantl 1887; Gray et al. 1889; Svenson 1943). Kükenthal's (1935–1936) subsequent reiteration of the same conclusion cemented the error, and the name *C. flavicomus* Michx. passed into effective obscurity—unrecognized in the literature for nearly a century until the work of Tucker (1985). With the nomenclatural histories of both names established, we proceed to a direct examination of the original material.

EXAMINATION

All protologues and, when available, original type materials examined for names circumscribed within Bentham's flatsedge, with the single exception of *C. macrostachyos* Lam., are consistent with a single species (Table 1). These types all present the spikelet characters diagnostic of Bentham's flatsedge—most notably the non-overlapping glume arrangement at maturity—differing from one another only in the environmentally plastic characters already addressed. The holotype of *P. albomarginatus* Mart. & Schrad. ex Nees was regrettably not available for examination; however, the protologue (Nees 1842) and later description of Tucker (1983) are fully consistent with the remaining types. Tucker (1985), who personally examined (on loan to DUKE herbarium) the holotypes of *albomarginatus* and *flavicomus,* noted of the latter "… it is clearly a plant of the species currently referred to as *C. albomarginatus*"; and the holotype of *C. flavicomus* Michx. ([P00667331]) clearly agrees with the wider Bentham's flatsedge concept. An 1839 collection identifiable with Bentham's flatsedge from the Brazilian state of Piauí (*Gardner #2384,* [K000189209]; cf. Kükenthal 1935–1936)—a contemporary plausible topotype of *C. albomarginatus*—can be used in conjunction with the descriptions and treatment of Nees (1842) and Tucker (1983, 1985) for the purposes of faithful examination.

The only departure warranting comment is that of *C. hochstetteri* var. *pinguior* C.B. Clarke, which presented glumes considerably longer than typical of the species (*Schimper #1551,* [K000363005]). In the protologue, C.B. Clarke (1886) was direct in his assessment: "Quamvis umbella, glumae nucesque iis C. Hochstetteri typici aliquanto majores videntur, revera tamen arcte congruent: species distincta esse vix potest" (although the umbels, glumes, and nuts appear somewhat larger than those of typical *C. hochstetteri,* in reality they nevertheless closely agree: it can scarcely be a distinct species). Kükenthal (1935–1936) later

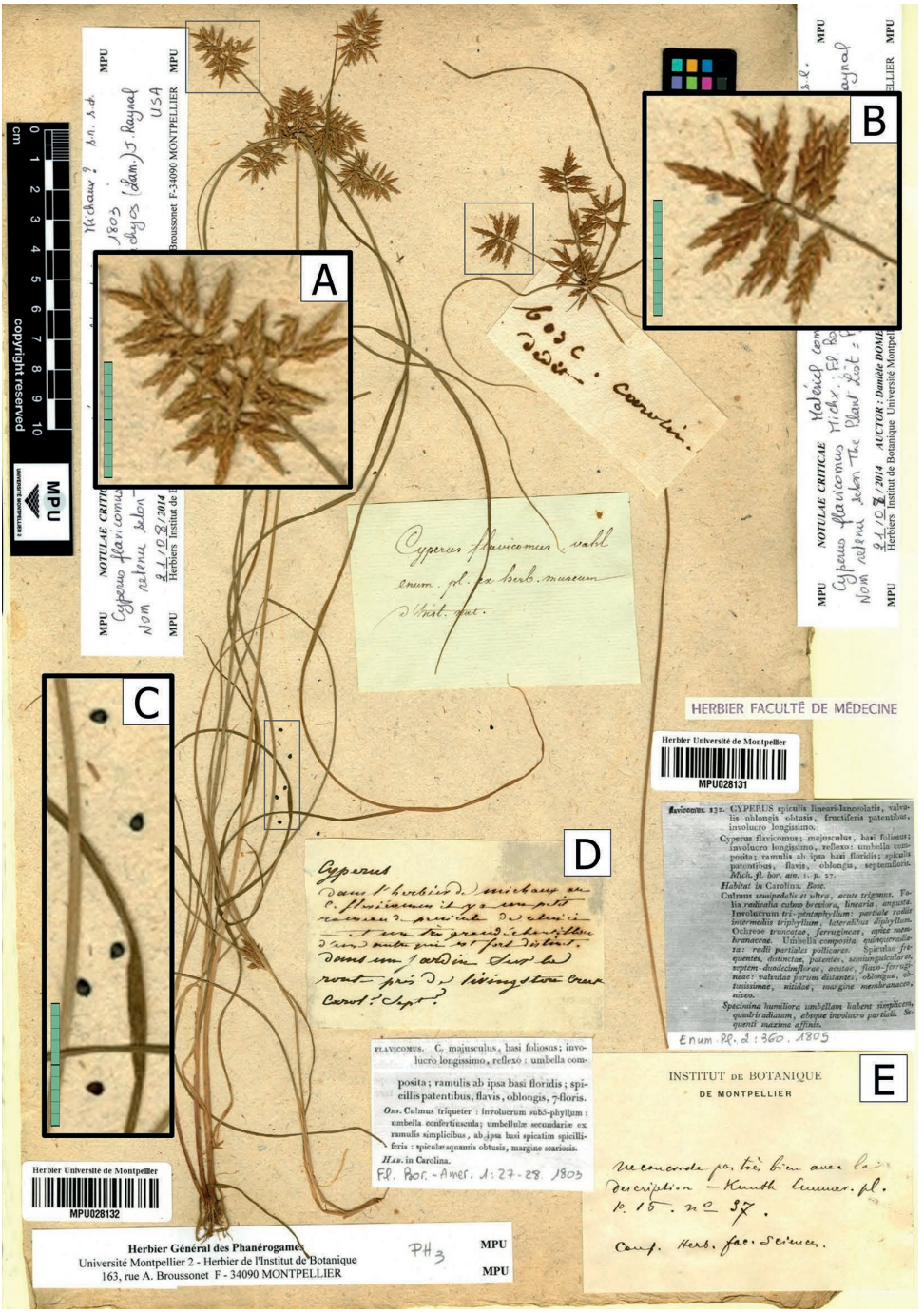


Fig. 12. An example of non-*flavicomus* "mixed material" described by Vahl (1805) for his description of *Cyperus flavicomus* (*L.A.G. Bosc #s.n.*, [MPU028131]). **A.** & **B.** Zoomed-in inflorescence of each specimen (scale = 1 cm). **C.** Achenes from a true specimen of *Cyperus flavicomus* Michx., an artifact of Vahl's original examination (scale = 1 cm). **D.** A note, potentially in Bosc's own hand, reading *"Cyperus,"* "dans l'herbier de Michaux au *C. flavicomus* il y a un petit rameau de panicule de celui-ci—et un grand échantillon d'un autre qui est fort distinct. dans un jardin sur la route près de livingstone creek. Carol? Sept? [likely 'Carolina? September?']" **E.** A later note reading "ne concorde pas très bien avec la description—Kunth Enumer. pl. p. 15. № 37."

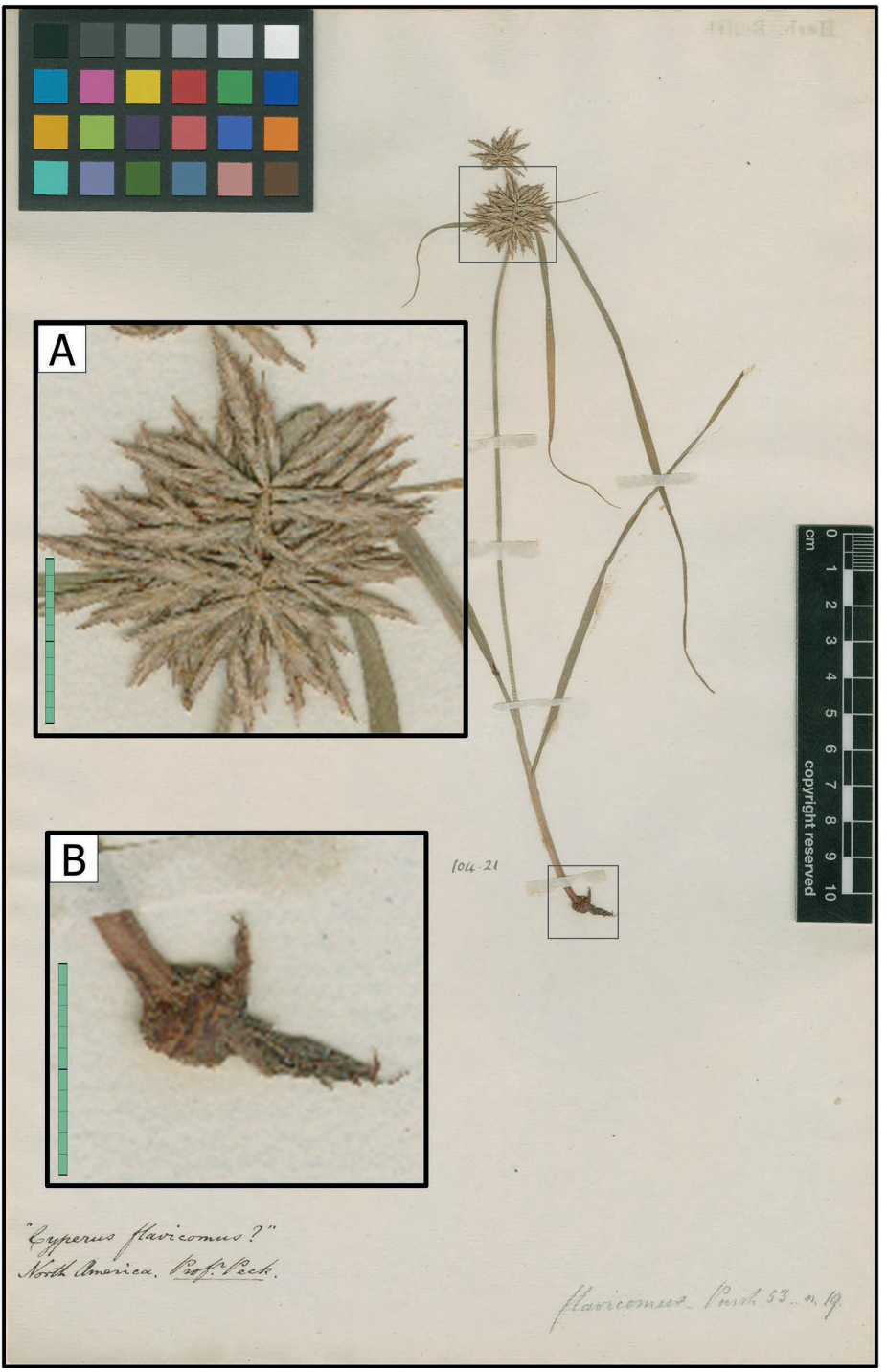


Fig. 13. The *Cyperus strigosus* L. specimen held at LINN causing C.B. Clarke's confusion regarding *Cyperus flavicomus* Michx.; at the time of writing still erroneously stored under the name *Cyperus flavicomus* Michx. (*Peck #s.n.*, [LINN-HS 104.21]). **A.** Zoomed-in inflorescence (scale = 1 cm). **B.** Zoomed-in swollen corm-like culm base, characteristic of *Cyperus strigosus* L. (scale = 1 cm).

TABLE 1. Diagnostic characters distinguishing Bentham's flatsedge (summarized under *Cyperus flavicomus* Michx., as treated here) from *C. macrostachyos* Lam. and *C. puncticulatus* Vahl, based on examination of original type materials (see Annotated Synonymy section; Appendices 1, 2, & 3).

Character	*C. flavicomus* Michx.	*C. macrostachyos* Lam.	*C. puncticulatus* Vahl
Achene color	Maturing brown–black	Maturing brown–black	Maturing brown–black
Achene shape	Obovate–oblong	Obovate	Obovate
Achene apex	Rounded–obtuse	Truncate–submarginate	Truncate–submarginate
Achene:glume length	≥ 2/3	≤ 1/2	≤ 1/2
Glume length (mm)	1.4–2.5	2.6–3.0	2.5–2.9
Glume keel excurrence	Commonly none; occasionally slightly mucronate below the apex.	Shortly mucronate below the apex.	Shortly mucronate below the apex.
Glume spread	Glumes spread widely as achenes mature until non-overlapping, gradually deciduous	Glumes more imbricate through maturity, suddenly deciduous	Glumes more imbricate through maturity, suddenly deciduous
Rachilla form	Subflexuous (loosely zigzagged)	Flexuous (zigzagged)	Flexuous (zigzagged)
Bracteole form	Filiform–setaceous, decreasing in length acropetally, typically exceeding the lowest fertile glume	Glumaceous, short, oblong	Glumaceous, short, oblong
Style division	Always deeply bifurcated (≥ 2/3 of length), often nearly from the style base	Shortly bifurcated (ca. 2/5 of length)[A]	Bifurcation variable: ≤ 1/3 of length (Koyama 1977: Fig. 7) to deeply bifid (Kük. 1935–1936)

[A]Only one intact style is conspicuous on the holotype sheet of *C. macrostachyos* Lam.

referenced *Schimper #1551,* the type of Clarke's var. *pinguior,* among the citations of *C. albomarginatus* without further remark. A 2004 collection from the same locality near Lake Tana, Ethiopia (*I. Friis et al. #11845,* [K002541272]) presents the same features: elongated glumes, but in all other structural characters—achene form, bracteole, glume arrangement at maturity—unambiguously Bentham's flatsedge.

Across the full range of examined types, every specimen presents the spreading, non-overlapping glume arrangement diagnostic of Bentham's flatsedge at maturity. Every type, that is, but one. The holotype of *C. macrostachyos* Lam. ([P00668535], and fragment [P00573081]) displays fully mature, darkened achenes still closely appressed by their subtending glumes—a condition unique, among original materials attributed to Bentham's flatsedge, to *C. macrostachyos*.

Closer examination reveals that the distinction extends well beyond glume arrangement (Table 1; Fig. 9). In the *C. macrostachyos* holotype and holotype fragment, the rachilla is strongly flexuous, producing a zigzag pattern that opens narrow windows between successive glumes through which mature black achenes are visible—but the glumes themselves remain imbricate, abscising individually shortly after achene maturity rather than progressively spreading as in Bentham's flatsedge. The *macrostachyos* bracteole is glumaceous, short, and oblong; in Bentham's flatsedge it is setaceous to filiform, often exceeding the lowest fertile glume. C.B. Clarke (1886) documented this same contrast between his *C. puncticulatus* ("bracteola parvula, oblonga, bracteaeformis") and *C. hochstetteri* ("bracteola lineari-subulata … glumam imam fertilem multum superans"). The achene apex of *macrostachyos* is truncate to subemarginate, as opposed to the more rounded, obtuse apex in achenes of Bentham's flatsedge. The undivided portion of the style is longer than the stigma branches in the holotype—a proportion never observed in Bentham's flatsedge, where the stigma branches are consistently the longer element, often bifurcating nearly at the style base. The glume keel is minutely mucronulate below the apex, visible where it juts out ever so slightly from the glume margin; in Bentham's flatsedge, this feature is variably present, and not discernible without magnification on intact glumes. The achene occupies approximately half or less of the glume length (≤ 1/2), compared with two-thirds or more in Bentham's flatsedge (≥ 2/3)—proportions documented by both Clarke (1886) and Kükenthal (1935–1936). Tucker (1985)—the only author documented to have personally examined the types of both *C. flavicomus* and *C. macrostachyos*—

independently reached the same conclusion, identifying the *C. macrostachyos* type with *C. puncticulatus* var. *quinquagintiflorus* C.B. Clarke sensu Kükenthal (1935–1936), citing Kunth (1837) in support.

The distinction holds well beyond the original type materials. The broader herbarium collections and field material examined for this study encompass the full geographic and morphological range of Bentham's flatsedge; yet no specimen referable to Bentham's flatsedge, from any continent, at any stage of development, matches the characters displayed by the *C. macrostachyos* holotype. Among the material surveyed, we did identify several specimens of Bentham's flatsedge with spikelets approaching the dimensions of the *C. macrostachyos* material, but side-by-side comparison of these specimens served only to sharpen the distinction (Fig. 14): invariably in Bentham's flatsedge, the glumes spread as achenes mature, the spikelet bracteoles are setaceous to filiform, the achene apex is more obtuse, the stigma branches far exceed the undivided portion of the style in length—a complete diagnostic suite, maintained regardless of spikelet or glume dimensions.

If *C. macrostachyos* is not Bentham's flatsedge, the question arises: what is it? The historical answer—*C. puncticulatus,* endemic to South Asia—was maintained in some sense from Kunth (1837) through to Kükenthal (1935–1936), but the "Ex Africa" locality ascribed to the original type material cannot be simply ignored. Rather than rely on the conclusions of previous authors, we undertook an independent survey of digitized African collections to determine whether any taxon on the continent could match the original type material of *C. macrostachyos* Lam.

Consulting the extensive African Cyperaceae treatments of Haines and Lye (1983) and of Hoenselaar et al. (2010) to establish reasonable bounds for such a considerable task—broad enough to capture any potential matches, narrow enough to realistically achieve—*C. macrostachyos* Lam. can be immediately narrowed to *Pycreus, Kyllinga,* or *Queenslandia* based on characters directly observable on the holotype material—the combination of bifid styles and lenticularly compressed achenes (notably excluding *Cyperus* s.s.—styles almost always trifid, achenes trigonous; styles rarely bifid but then with achenes dorsiventrally compressed). Hoenselaar et al. (2010) describe inflorescence structure in *Kyllinga* as "a single ovoid or globose spike, or a complex head with smaller lateral spikes at base of main spike"; far and away from the open, compound anthelodium with elongate, spreading spikelets presented by the *macrostachyos* type material. Furthermore, the deciduous nature of the *Queenslandia* spikelet unit where "[persistent] glumes are shed together with the rachilla" (Haines & Lye 1983) contrasts sharply with the persistent rachilla and gradually deciduous glumes presented by the *macrostachyos* holotype (Fig. 9). Our search can therefore be confidently confined to *Pycreus* material.

Among all digitized African collections of *Pycreus* surveyed for this study, none were compatible with Lamarck's "Ex Africa" material—two taxa in particular approach the holotype in certain characters, but differ irreconcilably in others. *Cyperus pelophilus* Ridl. does share the strongly flexuous rachilla, truncate achene apex, thin membranous glume margins, and tightly imbricate glumes that abscise individually at maturity rather than spreading gradually; however, the glumes are considerably smaller and more acutely tapered, and the keel is strongly excurrent well beyond the glume margin (*Welwitsch #7025,* [LISU224778]; *Welwitsch #7082,* [LISU224781]). The nearest candidate is *C. longistolon* Peter & Kük., a perennial with long-creeping stolons that is not uncommonly confused with Bentham's flatsedge in African collections (cf. *Terry #229,* [K002543260]; *Heath #2048,* [K002542437]; Greenway #7778, [K002541302]; *P.A. Smith #2994,* [K002543264]; *F.A. Rogers #5090,* [K002543228]; *Klaasen #EK262,* [US:02231025]). Indeed, in attempting to identify the *C. macrostachyos* types, we found that the keys of both Haines and Lye (1983) and Hoenselaar et al. (2010) lead to *C. longistolon* if the "Ex Africa" material is assumed to have come from such a perennial plant with long, slender stolons. The similarity here is not merely superficial; the molecular phylogeny of Larridon et al. (2013) recovered *C. longistolon* as a sister taxon to Bentham's flatsedge ("*C. macrostachyos*" in Larridon et al. 2013) with maximum support (posterior probability 1.00, bootstrap support 100). While identification with *C. longistolon* would certainly be satisfying for this study given the "Ex Africa" locality of Lamarck's material and the at-a-glance agreement in their achene morphology, hyaline glume margins, and glume arrangement, closer examination reveals that the two are distinguishable: the rachilla of *C. longistolon* is rigid and straight



Fig. 14. Comparison of *Cyperus macrostachyos* Lam. to long-spikeleted specimens of *Cyperus flavicomus* Michx. specifically selected for their similarity (scale = 1 cm). A. Holotype of *C. macrostachyos* Lam. (*s.c. #s.n.,* [P00668535]). B. From Louisiana, *J. Hale #s.n.,* [K002544102]. C. From Burundi, *J. Lewalle #1816,* [BR0000018189636].

("rigida exalata," Kükenthal 1935–1936) rather than flexuous; the glume apex is acute, with the keel typically projecting well beyond the glume body to produce a distinctly serrate spikelet outline, in contrast to the obtuse apex of the *macrostachyos* type with only a minute mucro below the tip; and the anthers are proportionally much longer relative to the filaments in *C. longistolon* than in the *C. macrostachyos* holotype. Moreover, both Clarke (1886) and Kükenthal (1935–1936) examined material of *C. longistolon, C. puncticulatus,* and Bentham's flatsedge, and maintained them as distinct taxa.

Given the already-doubtful provenance of Lamarck's material, the absence of any matching African taxon is telling—but it is the exhaustion of African candidates, not speculation, that compels us to look elsewhere. Colonial-era shipping records document extensive European maritime traffic connecting ports along the African coast with the Indian subcontinent via shared Indian Ocean routes throughout the 18th and early 19th centuries (García-Herrera et al. 2005); there is a distinct possibility that a South Asian specimen could have been mislabeled or intermixed with African collections somewhere along these converging routes. With this in mind, we extended our survey to include South Asian collections of *Pycreus*.

The identity of *C. macrostachyos* became immediately unmistakable. The holotype corresponds precisely—not approximately, not in general habit, but character for character—to collections of *C. puncticulatus* Vahl, most completely demonstrated by *Thwaites #3751* ([BR0000021904776]) and *R.G. Cooray #70032311R* ([US:02225358]), both from Sri Lanka (Fig. 15; cf. also Koyama 1977: Fig. 7). Every character that separated the *C. macrostachyos* holotype from Bentham's flatsedge unites it with *C. puncticulatus* as represented by these collections: glumes remaining closely imbricate at maturity, rachilla flexuous, bracteoles glumaceous and short, achene apices truncate, achene:glume proportion and achene form consistent throughout—the correspondence is consistent across all observable characters.

INTERPRETATIONS AND CONCLUSIONS

The morphological evidence is unambiguous: Lamarck's "Ex Africa" material is *C. puncticulatus* Vahl. This determination, reached through side-by-side comparison of the original material with digitized collections spanning the full geographic range of both Bentham's flatsedge and *C. puncticulatus,* is corroborated by every botanist documented to have independently examined the relevant materials: Vahl (1805), who matched Lamarck's fragment to Rottler's Indian specimen (itself reliably attributed to *C. puncticulatus* by all subsequent authors); Kunth (1837), who placed *C. macrostachyos* as a subspecies of *C. puncticulatus*; and Tucker (1985), who explicitly rejected Hooper and Raynal's treatment and aligned *C. macrostachyos* with *C. puncticulatus,* citing Kunth (1837) in support. Bentham's flatsedge and *C. puncticulatus* are not merely regional ecotypes of a single taxon—the anatomical work of Govindarajalu (1978), whose detailed cellular characterization of both species documents structural differences beyond those observable in gross morphology,



Fig. 15. Comparison of *Cyperus macrostachyos* Lam. and *C. puncticulatus* Vahl (scale = 1 cm). **A.** Holotype of *C. macrostachyos* Lam. (*s.c. #s.n.*, [P00668535]). **B.** From Sri Lanka, *C. puncticulatus* Vahl. (*Thwaites #3751*, [BR0000021904776]).

confirms them as genuinely distinct species. Moreover, the diagnostic distinctions presented here are consistent with those documented by Blatter and McCann (1934) and later Cook (1996) for Indian populations of both species.

The case against the "Ex Africa" provenance of the *C. macrostachyos* Lam. holotype is substantial. Consider the anomalous nature of its protologue among Lamarck's *Cyperus* entries, the early doubt surrounding the African locality—omitted entirely by A. Dietrich (1833) and D.N.F. Dietrich (1839), explicitly questioned by Kunth (1837); the effective abandonment of the name by the mid-nineteenth century; the inability of the present study to identify any matching material among digitized African collections of *Pycreus*; and the exact agreement of the original material with Indian and Sri Lankan collections of *C. puncticulatus*. Given that South Asian botanical collections routinely passed through African ports en route to European herbaria (cf. García-Herrera et al. 2005), the most parsimonious explanation is that the "Ex Africa" locality ascribed to *C. macrostachyos* was an error—a mislabeling or intermixing of specimens somewhere along the path from field to herbarium. Under Art. 9.24 of the ICN (Madrid Code, Turland et al. 2025), errors in the locality cited in a type designation are to be corrected, provided that the intent of the original author is not changed. Although Lamarck's "Ex Africa" locality has remained uncorroborated for over two centuries, we cannot exclude the possibility that an African population of *C. puncticulatus* has since been extirpated, or that matching material exists in collections not yet digitized. The locality of Lamarck's material is therefore not formally corrected here; however, following the precedent of Kunth's (1837) "? Africa," we render the locality citation as "Uncertain locality ('Ex Africa' teste Lamarck 1791)"—retaining the original claim while reflecting the compelling doubt surrounding its accuracy.

Concerning Bentham's flatsedge: the concept of a single, widely distributed species—first proposed by Bentham (Bentham & Mueller 1878), echoed by Wild and McEwen (1961), Hooper (1972), Hoenselaar et al. (2010), and Mesterházy et al. (2022), but never substantiated with comparison of original types—is here confirmed. The characters historically cited as diagnostic for its separation are, without exception, either environmentally plastic, maturity-dependent, or both. The correct name for the species is *C. flavicomus* Michx. (1803)—first restored from obscurity by Tucker (1985), here independently verified and now extended to encompass the full synonymy. [Note: for those disagreeing with Larridon et al. (2014) and those who prefer to maintain *Pycreus* at full genus rank, *P. albomarginatus* Mart. & Schrad. ex Nees (1842) has priority as the earliest name for Bentham's flatsedge within *Pycreus*.]

The validity of a published name is determined solely by the requirements of Art. 32–45 of the ICN (Madrid Code, Turland et al. 2025), none of which stipulate accurate locality data; only the type itself governs the application of the name. *C. macrostachyos* Lam. (1791)—being demonstrably conspecific with *C. puncticulatus* Vahl (1805)—has nomenclatural priority as the earliest published name for that species. However, adopting *C. macrostachyos* as the correct name for the South Asian species would replace a name that has been in stable, unambiguous use for over two centuries. Furthermore, because *C. macrostachyos* has been continuously misapplied to *C. flavicomus* s.l. (i.e., "Bentham's flatsedge") since Hooper and Raynal (1969), transferring the name to *C. puncticulatus* would create a situation in which "*C. macrostachyos*" simultaneously refers to the wrong species in all existing literature, and correctly to a separate species in all future literature—both members of the same subgenus that have long been considered closely related and are already routinely confused. This change would affect all post-1969 literature, multiple regional floras across four continents, global databases including POWO and the Global Cyperaceae Database, and would serve only to exacerbate the nomenclatural confusion for these species that we sought to resolve in the first place. We therefore recommend conservation of *C. puncticulatus* Vahl against *C. macrostachyos* Lam. under Art. 14 of the ICN (Madrid Code, Turland et al. 2025), a formal proposal for which will be submitted to Taxon. Pending the committee's decision, *C. puncticulatus* should continue to be used following Rec. 14A.1.

Nomenclatural consequences.—All modern records filed under *C. macrostachyos* (or *P. macrostachyos*) sensu Hooper and Raynal (1969)—that is, the *Pycreus* species with lenticularly flattened achenes, a bifid style, and non-overlapping, hyaline-margined glumes—should be transferred to *C. flavicomus* Michx. Records

from South Asia filed under *C. macrostachyos* s.l. should be evaluated on a specimen-by-specimen basis to determine whether they represent true *C. macrostachyos* (= *C. puncticulatus* Vahl., conservation proposed) or belong to *C. flavicomus*. As the name *C. macrostachyos* was completely out of use by the time of Hooper and Raynal's (1969) work reinstating its use, all post-1969 uses of the names *C. macrostachyos* or *P. macrostachyos* in the literature should be understood as references to *C. flavicomus*. To resolve as much confusion as possible, major references to and descriptions of these names are placed with the species to which they are here referred in the synonymy presented herein.

One group of names warrants particular scrutiny. *C. colchicus* K. Koch, *C. stachyphorus* K. Koch, and *P. woronowii* Palla—currently treated as the separate species *C. colchicus* (POWO 2026; cf. Egorova 1991 apud Vishnyakov & Verloove 2025)—have historically been treated as varieties or synonyms of *C. tremulus* (= *C. flavicomus*) by several authors (Boissier 1884; Komarov & Shischkin 1935; Kükenthal 1935–1936), and Palla (1912) explicitly described *P. woronowii* as "ex affinitate *P. hochstetteri*" (= *C. flavicomus*) in its protologue. Vishnyakov and Verloove (2025) recently rediscovered the species in the region after a documented gap of "more than 30 years of apparent absence" and lectotypified *P. woronowii* (*G. Woronow #620,* [GZU000012874]), providing the most detailed modern account of the Caucasian populations and confirming their continued —or perhaps recurrent—presence in the region. The specimens examined for the present study support this treatment: the lectotype and paralectotypes of *P. woronowii* and a later 1917 collection of Woronow's from the same region (*G. Woronow #s.n.,* [K002453792]) all display the conspicuous white glume margins and diagnostic non-overlapping glume arrangement at maturity characteristic of *C. flavicomus,* and recent field images attributed to *C. colchicus* from the Black Sea coast of Georgia (Vishnyakov 2023, available at https://www.inaturalist.org/observations/183831954) are fully consistent with *C. flavicomus* as circumscribed here. C.B. Clarke (1897), who personally examined Koch's material, reached the same conclusion—he found *C. colchicus* and *C. stachyphorus* to be conspecific with *P. tremulus,* and considered the Mascarene and Mingrelian plants "identical." Clarke did, however, find the species' Caucasian occurrence biogeographically inexplicable, remarking on the difficulty of explaining how such a tropical species could have reached and established itself in that region. Indeed, the Transcaucasian populations appear extremely isolated from the nearest known collection in Sudan, roughly 3000 km away (Fig. 16). This distributional disjunction, while not reflected in the morphology of the available specimens, does merit further investigation; we recognize a single species at present but recommend DNA barcoding to assess potential genetic differentiation in the Caucasian populations.

A cautionary lesson.—Two parallel errors, born of the same fundamental failure, have sustained nearly two centuries of nomenclatural confusion surrounding these species. In the case of *C. flavicomus*, Clarke's reliance on a single misidentified specimen—without consultation of Michaux's holotype—resulted in the neglect of a validly published name for nearly a century. In the case of *C. macrostachyos,* Hooper and Raynal assigned an incorrect name to a widely distributed species by examining the *C. macrostachyos* type in isolation, without cross-referencing it against the types of *P. albomarginatus* or any of the names they proposed to synonymize. In both cases, subsequent authors accepted the published determination at face value and perpetuated the error without returning to the original material—an understandable economy in an era of limited herbarium access, but one with lasting consequences.

The ease with which these errors were propagated—across decades and through the work of otherwise careful botanists—illustrates the value of type-based taxonomy and the importance of returning to primary material. Digital resources such as the JSTOR Global Plants Database, the Kew Data Portal, the MNHN image portal, GBIF, and SERNEC now make this kind of verification more accessible than at any point in the history of the discipline.

ANNOTATED SYNONYMY

In order to eliminate as much confusion as possible surrounding the nomenclatural history of *C. flavicomus,* each synonym has been annotated with references to all significant treatments or descriptions of the species

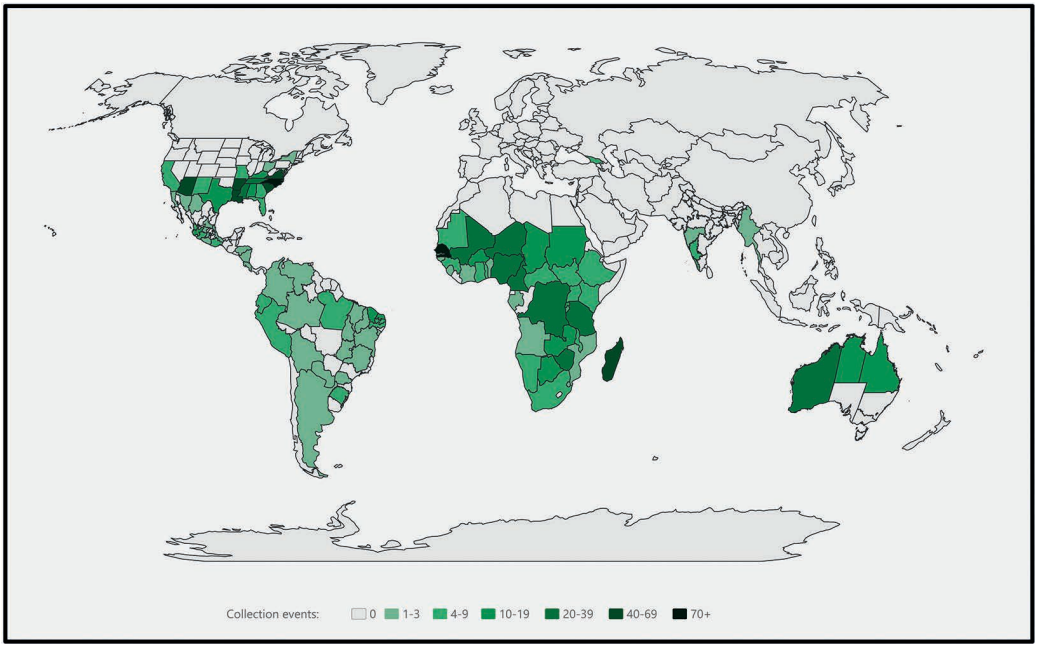


Fig. 16. Global distribution of *Cyperus flavicomus* Michx. based on examined herbarium collections (Appendices 1, 2) displayed as a choropleth map of unique collection events at national level, with subnational detail for Australia, Brazil, India, Mexico, and the United States of America.

under that name following the initial protologue citation; these citations are delimited by semicolons. The references are extensive but not exhaustive. Misapplications are cited as "auct. non" entries without type citations; "non" citations within an accepted or synonym entry indicate excluded references that used the same name for a different taxon. Where a specimen is known to exist but was not personally examined, the source of that information is cited as "fide Author Year." Type material that could not be located in any of the databases surveyed is cited as "not located." When the exact collection date is uncertain but the range can be approximated from knowledge of the collector's itinerary or from information present on the herbarium sheet, the approximated range is presented after "s.d." in curly brackets (e.g., s.d. {1836–1844}). A formal description of *C. flavicomus* follows the synonymy; *C. puncticulatus* Vahl and *C. macrostachyos* Lam. are treated separately below.

Cyperus flavicomus Michx., Fl. Bor.-Amer. 1:27. 1803; Poiret in J.B.A.M. de Lam., Encycl. 7:268. 1806; Muhlenberg, Descr. Gram. p. 24. 1817; Elliott, Sketch Bot. S. Carolina 1:71. 1821; Torrey, Ann. Lyc. N. York 3:253. 1836; Kunth, Enum. Pl. 2:15. 1837; Steudel, Syn. Pl. Glumac. 2:9. 1855; Torrey, Bot. Mexic. Bound. 226. 1859; A. Gray, Man. Bot. North. Unit. St. ed. 5:552. 1867; Boeckeler, Linnaea 35:470. 1868; Bentham & Mueller, Fl. Austral. 7:261. 1878; Britton, Bull. Torr. Bot. Club 13:206. 1886; Chapman, Fl. South. Unit. St. ed. 3:533. 1897; Small, Fl. S.E. U.S. ed. 2:166. 1913; Tucker, Rhodora 87:540. 1985; C.C. Baskin et al., Aquat. Bot. 45:41–52. 1993; Bryson & Carter, Sida 16:178. 1994; Diego-Pérez, Flora de Guerrero 5:53. 1997; Tucker in Stevens, Flora de Nicaragua 85(1):749. 2001; DiTomaso & Healy, Aquatic and Riparian Weeds of the West p. 183. 2003; Gómez-Laurito, Manual de Plantas de Costa Rica 2:483. 2003; Bryson & Carter in Naczi & Ford, Monogr. Syst. Bot. 108:44, 84. 2008; E.W. Chester et al., Guide to the Vascular Plants of Tennessee p. 251. 2015; C.C. Baskin et al., Plant Ecol. 220:734. 2019; non Pursh, Fl. Amer. Sept. 1:53. 1814; non Fern.-Vill. in Blanco, Fl. Filip. Gran ed. 4:301. 1880; non C.B. Clarke, J. Linn. Soc., Bot. 21:71. 1886; non Macoun, Cat. Canad. Pl. p. 94. 1888; non MacMillan, Metasp. Minnesota Valley p. 91. 1892; non C.B. Clarke in Hooker, Fl. Brit. India 6:594. 1894; non Kük. in H.G.A. Engler (ed.), Pflanzenr. IV, 20(101):407. 1936. *Pycreus flavicomus* (Michx.) C.D. Adams in Ann. Missouri Bot. Gard. 78:254. 1991. Type: U.S.A. Carolina: "Hab. in Carolina," s.d. {1786–1796}, *Michaux #s.n.* (holotype: [P00667331]!)

Cyperus flavicomus Vahl, Enum. Pl. 2:360. 1805, nom. superfl.; Britton, Bull. Torr. Bot. Club 13:206. 1886; C.B. Clarke, J. Linn. Soc., Bot. 21:71. 1886; Engler & Prantl, Nat. Pflanzenfam. Teil 2, Abt. 2:107. 1887; A. Gray, Man. Bot. North. Unit. St. ed. 6:569. 1889; C.B. Clarke in Hooker, Fl. Brit. India 6:594. 1894; Kük. in H.G.A. Engler (ed.), Pflanzenr. IV, 20(101):359. 1936. Type: U.S.A. South Carolina: Without locality, s.d., *Bosc #s.n.* (holotype: C, fide Tucker 1985)

Cyperus tremulus Poir. in J.B.A.M. de Lam., Encycl. 7:264. 1806; Kunth, Enum. Pl. 2:16. 1837; Steudel, Syn. Pl. Glumac. 2:10. 1855; Boeckeler, Linnaea 35:469. 1868; Baker, Fl. Mauritius p. 409. 1877; Boissier, Fl. Orient. 5:365. 1884; C.B. Clarke, J. Linn. Soc., Bot. 20:282. 1884; C.B. Clarke, J. Linn. Soc., Bot. 21:71. 1886; K. Schum. in H.G.A. Engler, Pflanzenwelt Ost-Afr. C:117. 1895; Kük. in H.G.A. Engler (ed.), Pflanzenr. IV, 20(101):361. 1936. *Pycreus tremulus* (Poir.) C.B. Clarke in T.A. Durand & H. Schinz, Consp. Fl. Afric. 5:542. 1895; Durand & Schinz, Etud. Fl. Congo 1:282. 1896; C.B. Clarke, J. Bot. 35:71. 1897; Clarke in Thiselt.-Dyer, Fl. trop. Afr. 8:306. 1902; H. Chermezon, Annal. Mus. Colon. Mars. XXVII. 3. Ser. 7:67. 1919; Chevalier, Explor. Bot. Afr. Occid. Franc. 1:696. 1920; Komarov & Shischkin, Flora of the U.S.S.R. 3:8. 1935; H. Chermezon in Humbert, Fl. Madagasc. fam. 29:48. 1937; Wild & McEwen, Kirkia 2:47. 1961; D.M. Napper, J. East Afr. Nat. Hist. Soc. Natl. Mus. 28:3. 1971; non H. Gillet & A. Vaillant, Bull. Mus. Natl. Hist. Nat. 29(3):285. 1957. *Pycreus macrostachyos* (Lam.) J. Raynal subsp. *tremulus* (Poir.) Lye in Nordic J. Bot. 1:622. 1981; Govaerts & Simpson, World Checklist of Cyperaceae p. 607. 2007. *Cyperus macrostachyos* Lam. subsp. *tremulus* (Poir.) Lye in R.W. Haines & K.A. Lye, Sedges and Rushes E. Afr., App. 3:2. 1983. Type: MADAGASCAR. "sur le bord des eaux," s.d., *du Petit-Thouars #s.n.* (holotype: [P00459829]!; holotype fragment: [P00459830]!).

Pycreus albomarginatus Mart. & Schrad. ex Nees in C.F.P. von Martius & auct. suc. (eds.), Fl. Bras. 2(1):9. 1842; C.B. Clarke in Hooker, Fl. Brit. India 6:594. 1894; C.B. Clarke in Durand & Schinz, Consp. Fl. Afric. 5:534. 1895; Durand & Schinz, Etud. Fl. Congo 1:280. 1896; Rendle, Catal. Afr. Pl. Welw. 2:107. 1899; C.B. Clarke in Thiselt.-Dyer, Fl. trop. Afr. 8:305. 1902; Domin, Bibl. Bot. Heft 85:418. 1915; H. Chermezon, Annal. Mus. Colon. Mars. XXVII. 3. Ser. 7:66. 1919; Chevalier, Explor. Bot. Afr. Occid. Franc. 1:695. 1920; C.E.C. Fischer in Gamble, Fl. Madras 9:1627. 1931; Blatter & McCann, J. Bombay Nat. Hist. Soc. 37:29. 1934; H. Chermezon in Humbert, Fl. Madagasc. fam. 29:48. 1937; D.M. Napper, J. East Afr. Nat. Hist. Soc. Natl. Mus. 28:3. 1971. [Note: The original name published by Nees used the spelling "*albo-marginatus*," not "*albomarginatus*"; however, because the epithet is formed of words that would not usually stand independently ("*albo-*" in this context being the combining form of "*albus*," functioning as a prefix modifying "*-marginatus*"), and the letters on either side of the hyphen are not the same, "*albo-marginatus*" does not fulfill the requirements necessary to maintain the hyphenated variant as outlined in Art. 60.12b of the ICN (Madrid Code, Turland et al. 2025).] *Cyperus albomarginatus* (Mart. & Schrad. ex Nees) Steud., Syn. Pl. Glumac. 2:10. 1855; Kük. in H.G.A. Engler (ed.), Pflanzenr. IV, 20(101):359. 1936; Svenson, Flora of Panama pt. 2, fasc. 2:286. 1943; I.M. Johnston, J. Arnold Arbor. 25:44. 1944; D.S. Correll & H.B. Correll, Aquatic and Wetland Plants of Southwestern United States p. 426. 1972; Tucker, Syst. Bot. Monogr. 2:70. 1983; Tucker, Rhodora 87:540. 1985. Type: BRAZIL. Piauí: "in campis provinciae Piauhiensis," s.d., *Martius #s.n.* (holotype: M, fide Tucker 1985).

Pycreus sabulosus Mart. & Schrad. ex Nees in C.F.P. von Martius & auct. suc. (eds.), Fl. Bras. 2(1):10. 1842. *Cyperus sabulosus* (Mart. & Schrad. ex Nees) Steud., Syn. Pl. Glumac. 2:10. 1855; Boeckeler, Linnaea 35:468. 1868; Britton & Brown, Ill. Fl. N. U.S. 1:300. 1913. *Cyperus albomarginatus* (Mart. & Schrad. ex Nees) Steud. var. *sabulosus* (Mart. & Schrad. ex Nees) Kük. in H.G.A. Engler (ed.), Pflanzenr. IV, 20(101):361. 1936. Type: BRAZIL. Amazonas: "in campis arenosis udis juxta lacum Coari, provinciae fluminis Nigri," Nov s.d., *Martius #18885* (lectotype, designated by Tucker 1985: M, fide Tucker 1985. Type photographs: C photo!, [W0337678] photo!).

Cyperus hochstetteri Nees ex Krauss, Flora 28:755. 1845, in nota; Steudel, Syn. Pl. Glumac. 2:11. 1855; Boeckeler, Linnaea 35:471. 1868; C.B. Clarke, J. Linn. Soc., Bot. 20:282. 1884; Small, Fl. S.E. U.S. ed. 2:166. 1913. Type: SUDAN. "in arena humida ad stagna pluvialia prope pagum Cordofanum Abu-Gerad," 24 Sep 1839, *Kotschy #52* (lectotype, **designated here**: [TUB-007269]!; isolectotypes: [BR0000009860933]!, [HEID-701326]!, [HOH-009005]!, [K000363006]!, [K000363007]!, [P01834989]!, [P01887213]!, [P01887214]!, [US:806285]!, [US:3648064]!, [US:02231894]!; paralectotypes: [BR0000008452429]!, [HEID-701327]!, [HOH-009006]!, [HOH-009007]!, [K000363004]!, [MO-1515488]!, [MPU028211]!, [P01834986]!, [P01887221]!, [P01887222]!, [P01887223]!, [P01887228]!, [TUB-007254]!, [TUB-007255]!, [TUB-007256]!, [TUB-007267]!, [TUB-007268]!, [US:3648063]!, [US:945558]!).

Cyperus colchicus K. Koch in Linnaea 21:623. 1848; Steudel, Syn. Pl. Glumac. 2:4. 1855; Boeckeler, Linnaea 35:468. 1868; Vishnyakov & Verloove, Willdenowia 55:119. 2025. *Pycreus colchicus* (K. Koch) Schischk. ex Grossh. in Fl. Kavkaza 1:152. 1928; Komarov & Shischkin, Flora of the U.S.S.R. 3:8. 1935. *Cyperus tremulus* Poir. var. *colchicus* (K. Koch) Kük. in H.G.A. Engler (ed.), Pflanzenr. IV, 20(101):362. 1936. Type: GEORGIA. Imeretiya: "Am Pferdeflusse in Imerien auf tertiarem und angeschwemmtem Boden," s.d. {1836–1844}, *K. Koch #s.n.* (lectotype, **designated here:** [B 10 0296611]!).

Cyperus stachyphorus K. Koch in Linnaea 21:623. 1848; Steudel, Syn. Pl. Glumac. 2:4. 1855. *Cyperus tremulus* Poir. var. *minor* Boeck. in Linnaea 35:470. 1868. Type: TÜRKİYE. Artaschin: "Am Ufer des schwarzen Meeres im Paschalik Trebisond," 20 Aug 1843, *K. Koch #1700* (lectotype, **designated here:** [B 10 0296610]!).

Cyperus retusus A. Rich., Tent. Fl. Abyss. 2:485. 1850. Type: ETHIOPIA. "In stagnis prope Gafta," 12 Sep 1839, *Schimper #1199* (lectotype, **designated here:** [P01887221]!; isolectotypes: [BR0000008452429]!, [HEID-701327]!, [HOH-009006]!, [HOH-009007]!, [K000363004]!, [MO-1515488]!, [MPU028211]!, [P01834986]!, [P01887222]!, [P01887223]!, [P01887228]!, [TUB-007254]!, [TUB-007255]!, [TUB-007256]!, [TUB-007267]!, [TUB-007268]!, [US:3648063]!, [US:945558]!).

Cyperus argyraeus Steud., Syn. Pl. Glumac. 2:11. 1855. TYPE: SENEGAL. Sénégambie: "in herbatis humidis sabulosis prope pagum Bakes regni Walo," Aug 1828, *Leprieur #s.n.* (LECTOTYPE, **designated here:** [P00573083]!; ISOLECTOTYPES: [BR0000018188325]!, [P00573082]!).

Cyperus retusus Nees ex Steud., Syn. Pl. Glumac. 2:11. 1855. *Pycreus retusus* (Nees ex Steud.) Nees ex C.B. Clarke, J. Linn. Soc., Bot. 21:71. 1886. TYPE: MAURITIUS. Without locality, s.d., *Herb. Sieber #7* (LECTOTYPE, **designated here:** [P01870794]!; ISOLECTOTYPES: [K000363062]!, [P00459964]!)

Cyperus tremulus Poir. var. *opulentus* Boeck. in W.C.H. Peters, Naturw. Reise Mossambique 2:535. 1864. TYPE: MOZAMBIQUE. Without locality, s.d., *Peters #s.n.* (HOLOTYPE: not located).

Cyperus patuliflorus Boeck., Linnaea 35:473. 1868; Boeckeler, Flora 62:546. 1879. *Chlorocyperus patuliflorus* (Boeck.) Rikli, Jahrb. Wiss. Bot. 27:563. 1895. TYPE: INDIA. Malabar: "North and South Concan," s.d., *J. Stocks #s.n.* (LECTOTYPE, **designated here:** [K000592585]!; ISOLECTOTYPES: [P01714704]!, [P01714705]!).

Cyperus ornatissimus F. Muell., Fragm. 8:265. 1874. TYPE: AUSTRALIA. Northern Territory: "Gram's Range, Head of Sturt's Creek," s.d., *F. Mueller #s.n.* (LECTOTYPE, **designated here:** [MEL247992]!; PARALECTOTYPES: [K000881556]!, [MEL247991]!).

Cyperus hochstetteri Nees ex Krauss var. *tenuis* Boeck., Flora 62:546. 1879. *Cyperus albomarginatus* (Mart. & Schrad. ex Nees) Steud. var. *tenuis* (Boeck.) Kük. in H.G.A. Engler (ed.), Pflanzenr. IV, 20(101):361. 1936. *Pycreus macrostachyos* (Lam.) J. Raynal var. *tenuis* (Boeck.) Wickens, Kew Bull., Addit. Ser. 5:165. 1976. TYPE: SOUTH SUDAN. Iter Centrali-Africanum: "grosse Seriba Ghattas, in Lande der Djur," 5 Jun 1869, *Schweinfurth #*2018 (LECTOTYPE, **designated here:** [K000363008]!; ISOLECTOTYPES: [P01887206]!, [S13-17825]!).

Cyperus esculentus auct. non L.: Ridl. in Trans. Linn. Soc. 2. Ser. Bot. II:138. 1884, pro parte (fide Kükenthal 1935–1936).

Cyperus hochstetteri Nees ex Krauss var. *russa* C.B. Clarke, J. Linn. Soc., Bot. 20:282. 1884. TYPE: MAURITIUS. Without locality, s.d. 1858, *Grey #s.n.* (LECTOTYPE, **designated here:** [K000363061]!; PARALECTOTYPE: not located).

Cyperus hochstetteri Nees ex Krauss var. *pinguior* C.B. Clarke, J. Linn. Soc., Bot. 21:70. 1886. TYPE: ETHIOPIA. Begemder Etak: "near Lake Tana," s.d. 1863, *Schimper #*1551 (LECTOTYPE, **designated here:** [K000363005]!; ISOLECTOTYPE: [US:945721]!).

Pycreus albomarginatus Mart. & Schrad. ex Nees var. *bromoides* C.B. Clarke, Bull. Herb. Boissier 6 [App. 1]:19. 1898. TYPE: PARAGUAY. Without locality: "In palude prope Tucangua," Jan s.d. {1885–1892}, *Hassler #*1829 (HOLOTYPE: not located).

Pycreus woronowii Palla, Vestn. Tiflissk. Bot. Sada 21:22. 1912; Vishnyakov & Verloove, Willdenowia 55:121. 2025. *Cyperus tremulus* Poir. var. *woronowii* (Palla) Kük. in H.G.A. Engler (ed.), Pflanzenr. IV, 20(101):362. 1936. TYPE: GEORGIA. Lazistania: "Batumi, in paludosis prope p. Gonieh, loco Chuštule," 27 Aug 1910, *Woronow #620* (LECTOTYPE, designated by Vishnyakov & Verloove 2025: [GZU000012874] image!; ISOLECTOTYPES: [ERE 0005501] fide Vishnyakov & Verloove 2025, LE? fide Vishnyakov & Verloove 2025, [TBI 1054403] fide Vishnyakov & Verloove 2025; PARALECTOTYPES: [GZU000012877]!, [GZU000012876]!, [GZU000012875]!).

Cyperus albomarginatus (Mart. & Schrad. ex Nees) Steud. var. *pachyanthemos* Kük. in H.G.A. Engler (ed.), Pflanzenr. IV, 20(101):361. 1936. TYPE: PARAGUAY. Itacurubí: "Barranca Río Paraguay," Dec 1916, *Rojas #*2286A (HOLOTYPE: [SI000242]!).

Cyperus macrostachyos auct. non Lam.: Govindarajalu, Adansonia 18:106. 1978; Haines & Lye, Sedges and Rushes E. Afr. p. 288. 1983; Guaglianone in Zuloaga & Morrone, Monogr. Syst. Bot. 60:155. 1996; Bryson & Carter in Naczi & Ford, Monogr. Syst. Bot. 108:89. 2008; I. Larridon et al., Bot. J. Linn. Soc. 172:106–126. 2013; C.S. Reid et al., Pl. Ecol. Evol. 150(3):352. 2017; I. Semmouri et al., Bot. Rev. 85:19. 2018; Pereira-Silva et al., Ann. Mo. Bot. Gard. 107:520. 2022.

Pycreus macrostachyos auct. non (Lam.) J. Raynal: J. Raynal, Mitt. Bot. Staatssamml. München. 10:595. 1971; Hooper in Hutchinson, Fl. West Trop. Afr. 3:301. 1972; C.D.K. Cook, Aquatic and wetland plants of India p. 169. 1996; Guaglianone in Zuloaga & Morrone, Monogr. Syst. Bot. 60:178. 1996; D.E. Johnson, Les adventices en riziculture en Africa de l'Ouest p. 114. 1997; Jørgensen & León-Yanez, Monogr. Syst. Bot. 75:432. 1999; Valverde et al., Weed Sci. 49:398. 2001; Govaerts & Simpson, World Checklist of Cyperaceae p. 606. 2007; Bryson & Carter in Naczi & Ford, Monogr. Syst. Bot. 108:44, 84. 2008; Hoenselaar et al. in H.J. Beentje, Fl. Trop. E. Afr.: Cyperaceae. 2010; Leite et al., Braz. J. Biol. 72:163–169. 2012; Y. Kassa et al., Aquat. Bot. doi: 170:103351. 2021; Behn et al., Phytocoenologia 51(3):199–219. 2022; A. Diallo et al., J. Res. Weed. Sci. 5(2):105–117. 2022; A. Mesterházy et al., Cyperaceae of tropical West Africa p. 399. 2022.

Description.—Robust annual, up to 110 cm tall at maturity; **Roots** fibrous, dark-red with occasional white strands (rhizomes, tubers, and stolons absent); **Culms** solitary or caespitose, trigonous, (7–)30–75 cm × 1–5 mm, base fleshy to the touch, the lower quarter to half loosely covered by membranous reddish-brown leaf-bases, splitting as the culms grow, becoming pierced by new buds and emergent roots; **Leaves** three-ranked, linear, V-shaped, 5–60 cm × 1–9 mm, acuminate, apex loosely scabrid, eligulate, marcescent with age; **Inflorescence** a lax anthelodium, compound or ± decompound, seldom "simple" in the strict sense; **Primary rays** 3–6(–12), 1–15(–20) cm long, glabrous, their bases enclosed in a conspicuous tubular (pale) red-brown prophyll; **Involucral bracts** leaflike, erect or spreading, the largest (2–)8–35 cm × (1–)4–10 mm; **Involucellar bracts** 1–5 cm long, much narrower; **Spikelets** (3–)10–30(–many) per cluster, loosely spread along a pedunculate rachis, linear–(narrow)lanceolate, flattened, each with a glumaceous prophyll and filiform–setaceous bracteole 1–5 mm long (decreasing in length acropetally); **Rachilla** 0.3–0.5 mm wide, subflexuous, narrowly

winged; **Glumes** (floral scales) (ob)ovate, (1.4–)1.5–2.4(–3.0) mm × 0.8–1.6 mm, (golden) yellow to reddish-brown, laterally compressed, distichously arranged, non-overlapping at maturity, with a distinct whitish-hyaline margin about 0.3 mm wide; **Keel** green, 3–5-veined, rarely minutely excurrent; **Stamens** 2–3, filaments 1.8–2.6 mm long, anthers 0.4–0.9 mm long; **Styles** shortly exserted, deeply bifid; **Achenes** (nutlets) lenticularly flattened, (asymmetrically-)obovate–oblong, cuspidate, 1.4–2.2(–2.5) mm × 0.6–1.3 mm, pale brown maturing to jet black, surface with minute papillae in distinct longitudinal rows. Facultative wetland plant, typically preferring seasonally flooded habitats such as mudflats, marshes, or rice fields. **Distribution:** see Fig. 17; Appendices 1, 2.

Cyperus puncticulatus Vahl, Enum. Pl. Obs. 2:348. 1805; Roemer & Schultes, Syst. Veg. 2:206. 1817; A. Dietrich, Sp. Pl. 2:280. 1833; Kunth, Enum. Pl. 2:15. 1837; D.N.F. Dietrich, Syn. Pl. 1:216. 1839; Steudel, Nomencl. Bot. (ed. 2) 2:472. 1841; Steudel, Syn. Pl. Glumac. 2:10. 1855 (excl. syn. Roxb.); Dalzell & Gibson, Bomb. Fl. p. 283. 1861; Boeckeler, Linnaea 35:472. 1868; C.B. Clarke, J. Linn. Soc., Bot. 21:68. 1886; Ridley, Fl. Malay Penins. 5:140. 1925; Blatter & McCann, J. Bombay Nat. Hist. Soc. 37:29. 1934; Kük. in H.G.A. Engler (ed.), Pflanzenr. IV, 20(101):362. 1936; Govindarajalu, Adansonia 18:113. 1978. *Pycreus puncticulatus* (Vahl) Nees in C.F.P. von Martius & auct. suc. (eds.), Fl. Bras. 2(1):10. 1842, in obs.; C.B. Clarke in Hooker, Fl. Brit. India 6:593. 1894; C.E.C. Fischer in Gamble, Fl. Madras 9:1626. 1931; C.D.K. Cook, Aquatic and wetland plants of India p. 170. 1996. TYPE: INDIA. "Indiae orientalis aquosis," s.d., *s.c. #s.n.* (SYNTYPES: [C10010313]!, [C10010314]!).

Cyperus macrostachyos Lam., Tabl. Encycl. 1:147. 1791; Poiret in J.B.A.M. de Lam., Encycl. 7:268. 1806; Roemer & Schultes, Syst. Veg. 2:206. 1817; A. Dietrich, Sp. Pl. 2:281. 1833; D.N.F. Dietrich, Syn. Pl. 1:216. 1839; Steudel, Nomencl. Bot. (ed. 2) 2:470. 1841. {Note: *C. macrostachyos* Lam. has nomenclatural priority over *C. puncticulatus* Vahl but has been continuously misapplied to *C. flavicomus* Michx. since Hooper & Raynal 1969. Conservation of *C. puncticulatus* against *C. macrostachyos* Lam. is proposed herein; a formal proposal will be submitted to Taxon. Pending the committee's decision, *C. puncticulatus* Vahl is retained as the accepted name following Rec. 14A.1 of the ICN (Madrid Code, Turland et al. 2025).} *Cyperus macrostachyos* sensu Vahl, Enum. 2:349. 1805. *Cyperus puncticulatus* var. *macrostachyus* Kunth, Enum. Pl. 2:16. 1837. *Pycreus macrostachyos* (Lam.) J. Raynal, Kew Bull. 23:314. 1969, excl. syn. TYPE: Uncertain locality ("Ex Africa" teste Lamarck 1791), s.d., *s.c. #s.n.* (HOLOTYPE: [P00668535]!; HOLOTYPE FRAGMENT: [P00573081]!).

Cyperus puncticulatus Vahl var. *quinquagintiflorus* C.B. Clarke in J. Linn. Soc., Bot. 21:69. 1886; Kük. in H.G.A. Engler (ed.), Pflanzenr. IV, 20(101):363. 1936. *Pycreus puncticulatus* (Vahl) Nees var. *quinquagintiflorus* (C.B. Clarke) C.B. Clarke in J.D. Hooker, Fl. Brit. India 6:594. 1894. TYPE: INDIA. "India orientali," s.d., *Rottler #s.n.* (HOLOTYPE: not located).

Note.—A formal redescription of *C. puncticulatus* is not necessary; such a task would be beyond the scope of this work and inadequate without physical material for examination.

LECTOTYPE JUSTIFICATIONS

The synonymy established above designates lectotypes for 11 names. In selecting lectotypes, we prioritized sheets with evidence of direct provenance to the describing author—original labels, herbarium stamps, or handwritten determinations linking the specimen to the protologue. Where no sheet could be confidently connected to the author, we selected the most complete and representative specimen. Because we were uncertain as to whether additional original material of *C. puncticulatus* exists undigitized at C, we chose not to designate a lectotype for *C. puncticulatus*; the syntypes available for examination appear to be two halves of the same plant (i.e., perhaps a single specimen mounted across two sheets rather than two separate gatherings), but this is unconfirmable without physical examination or accompanying notes.

Cyperus hochstetteri.—*Schimper #1199* overlaps as original material between *C. hochstetteri* and *C. retusus* A. Rich., but *C. hochstetteri* was also described from *Kotschy #52*. Of the numerous duplicates of *Kotschy #52,* the sheet held at TUB ([TUB-007269]) could easily have been personally examined by Nees, possesses what appears to be Kotschy's original label for the collection, and has a handwritten correction to "*Cyperus Hochstetterianus* Nees ab Esenb."—very likely Nees' manuscript name that Krauss (1845) refers to in the unwitting "in nota" protologue ("… a Neesio in litteris ad me scriptis *C. Hochstetteri* …"). Additionally, [TUB-007269] bears two specimens at different stages of maturity, making the sheet invaluable as reference material. As such, this sheet was chosen for lectotypification. Basing the lectotype of *C. hochstetteri* on *Kotschy #52* rather than *Schimper #1199* also cleanly separates the typification of *C. hochstetteri* from that of *C. retusus* A. Rich., for which *Schimper #1199* is the only original material.

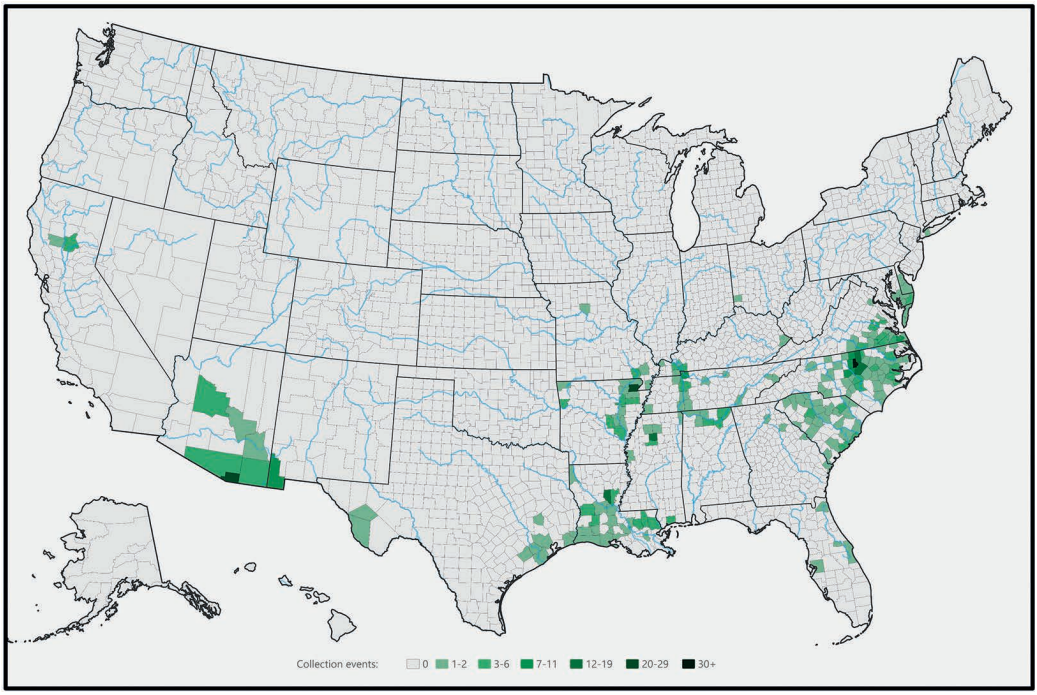


Fig. 17. Distribution of *Cyperus flavicomus* Michx. in the United States of America based on examined herbarium collections (Appendix 1), displayed as a choropleth map of unique collection events at state and county level.

***C. colchicus* and *C. stachyphorus*.—**The lectotypes chosen for *C. colchicus* and *C. stachyphorus* are the original materials described by Koch. Both bear labels of "Herbarium Karl Koch," "Original!," and "Linnaea XXI (1848) p. 623." The lectotypification of these collections is merely a formality.

***C. retusus* A. Rich.—**Achille Richard, a French botanist based in Paris, likely referenced one of the *Schimper #1199* duplicates held at P for his protologue. As such, [P01887221] was chosen for lectotypification because of its excellent representation of the characteristic non-overlapping glume architecture, clear filiform–setaceous bracteoles, and bearing a complete unaltered specimen with intact roots and culm.

***C. argyraeus*.—**Of the *Leprieur #s.n.* duplicates, [P00573083] bears the most extensive material, so it was chosen for lectotypification.

***C. retusus* Nees ex Steud.—**Of the *Sieber #7* duplicates, only [P01870794] bears the note "Herbarium Steudel" and an explicit determination of "*Cyperus retusus* Nees" rather than "Nees ex Steud." or simply "Steudel." This is clearly the specimen Steudel examined for the protologue, and thus it was chosen for lectotypification.

***C. patuliflorus*.—**None of the *J. Stocks #s.n.* duplicates stood out in terms of provenance or likelihood of personal examination from Boeckeler. [K000592585] was chosen as the lectotype on the basis of its more detailed labeling and examination history.

***C. ornatissimus*.—**Of the three syntypes, [MEL247992] is completely intact, in excellent condition, and has achenes separated and preserved in a plastic pouch on the sheet, making them easily accessible for examination. For these reasons, [MEL247992] was chosen as the lectotype.

***C. hochstetteri* var. *tenuis*.—**Of the *Schweinfurth #2018* duplicates, only [K000363008] possesses an explicit determination of "*Cyp. Hochstetteri* Nees var. *tenuis* Boeck.," so it was chosen for lectotypification.

***C. hochstetteri* var. *russa*.—**Of the two syntypes, we were only able to locate *Grey #s.n.* The specimen was in excellent condition and thus it was chosen for lectotypification.

***C. hochstetteri* var. *pinguior*.—**Of the two *Schimper #1551* duplicates, only [K000363005] bears a handwritten determination from C.B. Clarke and an explicit label of "*Cyperus Hochstetteri,* Nees. var. β *pinguior,* C.B. Clarke," so it was chosen for lectotypification.

VOUCHER-BACKED DISTRIBUTION

Based on the extensive material examined for this work, a verified, voucher-backed global distribution of *C. flavicomus* Michx. can be presented for the first time (Figs. 16, 17). A detailed discussion of the species' dispersal history—including the probable roles of the West African rice trade and migratory waterbird flyways in shaping its current distribution—will be addressed in a future publication. The maps are included here as a reference for future works and to provide corrections for existing databases.

These maps represent the documented historical range of the species as characterized by botanical collections, not necessarily the current distribution. Some records represent introductions that have not persisted—for example, in New York (Mitchell & Tucker 1997); the single known collections from Myanmar and Ohio likely represent similar transient occurrences. Several specimens that would have provided range extensions could not be examined and were excluded—most notably from Panama (cf. Tucker 1983, *Tyson & Clewell #5907*). Conversely, the absence of records from the Antilles, Southeast Asia, Polynesia, and the Guianas appears to reflect genuine absence rather than collection artifact; extensive effort was made to locate material from these regions, but no digitized specimens of *C. flavicomus* could be found. The Checklist of the plants of the Guiana Shield, for example, indeed records the species only from Bolívar, Venezuela (Camelbeke et al. 2007). Similarly, the apparent absence from Liberia, Equatorial Guinea, and adjacent regions may represent actual gaps in the species' African distribution, though collection bias cannot be ruled out.

The Transcaucasian occurrences, previously attributed to the separate species *C. colchicus* K. Koch, represent a striking distributional disjunction discussed earlier in this work. The biogeographic implications of these populations will be explored in the aforementioned future publication.

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ARTIFICIAL INTELLIGENCE DISCLAIMER

All text in this manuscript was written by the authors. Artificial intelligence tools (Grammarly AI, Grammarly Inc.; Claude Opus 4.6, Anthropic PBC) were used to suggest edits for grammar and clarity; all revisions were made manually by the authors. The code used to generate the distribution maps (Figs. 16, 17) was written by Claude Opus 4.6 under the direction and specifications of the first author, as described in Materials and Methods. Artificial intelligence tools did not contribute to data collection, specimen examination or identification, interpretations, or conclusions in any way.

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APPENDIX 1

United States Specimens

Appendix 1 contains a list of materials examined from the United States of America, organized by state and county. All materials listed were examined by the authors; as such, the customary "!" notation is not included. An abbreviated citation format excluding verbatim locality has been chosen for reasons of practicality; enough information is present that any specimen can be easily located using its given institution barcode through the relevant data portal. The collections are formatted as follows: **COUNTRY. STATE. County:** *Name #Number*, [Institution Barcode 1] [Institution Barcode 2] [etc.]. Unique collection events are separated by semicolons, and the last entry for any particular region ends with a period. When state or county locality information were not present or unclear on the label for any given sheet, they are listed under "Uncertain." A large portion of collections bore only handwritten labels; we apologize for any mistakes of transliteration. If any content was truly obscured, this is denoted in curly brackets as *"{obscured}."*

UNITED STATES OF AMERICA. ALABAMA. Jackson: *D.H. Webb #3506,* [FLAS:257190]; *D.H. Webb #7860*, [APSC0041536] [TENN-V-0039306]; *D.H. Webb et al. #1813*, [BRIT164549]. **Lauderdale:** *D.H. Webb & W.M. Dennis #3518*, [BRIT164550] [FSU:138713] [TENN-V-0039307]. **Lawrence:** *D.H. Webb & D. Murphy #4707*, [BRIT164551]. **Limestone:** *D.H. Webb & W.M. Dennis #2456*, [BRIT164552] [TENN-V-0039308]; *R. Kral #41225*, [BRIT164553] [SAT0035132]. **Marshall:** *D.H. Webb #3584b*, [FSU:138715] [TENN-V-0039310]; *D.H. Webb #4331*, [BRIT164555] [TENN-V-0039309]; *D.H. Webb & W.M. Dennis #3584b*, [BRIT164554]. **Morgan:** *R. Kral #41198*, [MBM132626] [DUKE10041890] [SAT0035134] [SWSL001378] [UNA00001103] [WILLI:50291]; *D.H. Webb & W.M. Dennis #3636*, [BRIT164557]; *D.H. Webb & W.M. Dennis #3637*, [FSU:138710] [TENN-V-0039312]; *R. Kral #41190*, [BRIT164558]; *R. Kral #54424*, [APSC0036014] [BRIT164556] [FSU:138708] [TENN-V-0039311] [VSC0045446]. **ARIZONA. Cochise:** *C. Roll #2307*, [ARIZ:430366] [ASU0307826]; *C. Roll #2968*, [ASC00125086]; *G. Clifton #47872*, [ASC00123868]; *G. Clifton #47919*, [ASC00123869]; *J.E. Laferriere #2626*, [EIU011122]; *S. Carnahan et al. #1415*, [ARIZ:428216] [ASC00116051]. **Gila:** *D.Z. Damrel et al. #V-633*, [TEUI0002644]; *T. Heggie #25*, [TEUI0002645] [USFS0072083]. **Graham:** *Pinkava et al. #15146*, [ASU0085012] [MICH:1393529]. **Pima:** *D. Beckman & N. Gonzalez #307*, [ARIZ:443416]; *F.W. Gould #3947*, [COLO:01067701] [MICH:1393530] [NY:2814424] [RSA0365420] [US:3155357]; *S. Rutman #20130925-4*, [ARIZ:415895]; *T.H. Kearney & R.H. Peebles #13785*, [US:1729442]. **Santa Cruz:** *S. Carnahan #4896*, [ARIZ:442351] [ASU0348303]; *D. Wolkis et al. #919*, [ASU0294053]; *P.L. Keil et al. #9825*, [ASU0085009] [OBI146346]; *E.R. Blakley #6223*, [DES00002072]; *J. Dash et al. #498*, [DES00096987]; *J. Kaiser #499*, [RSA0116307]; *L. Goodding #4988*, [ASU0085010]; *L. Makings et al. #7082a*, [ASU0312251]; *M. Licher #6377*, [ASC00129123]; *M. Licher #6386*, [ASC00129103]; *M. Licher & S. Carnahan #5735*, [ASC00121488]; *R.F. Thorne & C.W. Tilforth #59427*, [ARIZ:403736] [ASU0082008] [RSA0365419]; *S. Carnahan #1491*, [ARIZ:428126] [ASC00111669]; *S. Carnahan #1979*, [ARIZ:433501] [ASC00115162] [ASU0307728]; *S. Carnahan #2691*, [ARIZ:435879] [USON:29882]; *S. Carnahan #3938*, [ARIZ:444773]; *S. Carnahan #4569*, [ARIZ:441820]; *S. Carnahan #4895*, [ARIZ:442387]; *S. Carnahan & C. Smith. #3390*, [ARIZ:439459]; *S. Carnahan et al. #172*, [ASU0085011] [USON:21244]; *T.H. Kearney #14480*, [NY:2814407]; *W.C. Hodgson et al. #12746*, [DES00047621]; *W.C. Hodgson & D. Damrel #20797*, [DES00057514]; *T.H. Kearney & R.H. Peebles #14480*, [US:1768731] [US:1768730]. **Yavapai:** *M. Licher #6330*, [ASC00128919]; *M. Licher #6361*, [ASC00129114]; *M. Licher #6368*, [ASC00129119]; *M. Licher #6538*, [ASC00130000]. **ARKANSAS. Arkansas:** *B. Bauman & G. Beckwith #s.n.*, [AWS-2024-030]; *G. Wilks & J. Coleman #s.n.*, [AWS-2024-033]; *A.D. Ross & N.C. Chandler #s.n.*, [AWS-2025-016]; *R.H. Smith #2*, [US:3603806]; *N. Hotchkiss #7587*, [US:3605472]. **Benton:** *G. Templeton #s.n.*, [UARK049898]. **Clay:** *s.c. #s.n.*, [AWS-2023-013]. **Craighead:** *D. Demaree #31662*, [MICH:1393531]. **Crawford:** *C.T. Bryson #16061*, [ANHC005799] [SWSL001557] [VSC0004856] [NY:2814422]; *J.W. King #s.n.*, [SAT0037336]; *J.W. King #s.n.*, [SWSL001556]; *J.W. King #s.n.*, [UARK081422]; *J.W. King #s.n.*, [VSC0045447]. **Greene:** *S. Speer & D. Freeze #s.n.*, [AWS-2023-025]; *G. King & D. Freeze #s.n.*, [AWS-2023-040]; *S. Finch & D. Freeze #s.n.*, [AWS-2024-206]; *S. Henson & D. Freeze #s.n.*, [AWS-2024-207]; *M. Graham & D. Freeze #s.n.*, [AWS-2024-213]; *C. Ovick & D. Freeze #s.n.*, [AWS-2024-214]; *K. Randleman & D. Freeze #s.n.*, [AWS-2024-215]; *C. Davis & D. Freeze #s.n.*, [AWS-2024-221]; *J. Distretti & D. Freeze #s.n.*, [AWS-2025-124]; *J. Smith & D. Freeze #s.n.*, [AWS-2025-125]; *D. Rice & D. Freeze #s.n.*, [AWS-2025-126]; *S. King & D. Freeze #s.n.*, [AWS-2025-127]; *B. Martin & D. Freeze #s.n.*, [AWS-2025-128]; *S. Speer & D. Freeze #s.n.*, [AWS-2025-129]; *D. Boling & D. Freeze #s.n.*, [AWS-2025-130]; *Gray #s.n.*, [AWS-2023-117]; *C. Eason & M. Simmons #s.n.*, [AWS-2024-196]; *J. Smith & M. Simmons #s.n.*, [AWS-2024-197]; *F. Gates & M. Simmons #s.n.*, [AWS-2024-198]; *s.c. #s.n.*, [AWS-2024-222]. **Jackson:** *R. Chlapecka #s.n.*, [AWS-2023-016]; *R. Chlapecka #s.n.*, [AWS-2023-017]; *A.D. Ross & N.C. Chandler #s.n.*, [AWS-2025-015]. **Lawrence:** *R. Jacobs & C. Sisk #s.n.*, [AWS-2023-041]; *Wall & C. Sisk #s.n.*, [AWS-2023-042]. **Lonoke:** *K. Johnston & S. Baside #s.n.*, [AWS-2024-146]; *K. Johnston & S. Baside #s.n.*, [AWS-2024-148]; *K. Johnston & T. Padgett #s.n.*, [AWS-2024-195]. **Monroe:** *C.M. Halbrook & H.M. Houser #s.n.*, [AWS-2025-018]. **Poinsett:** *B. Lindsey & C. Duckworth #s.n.*, [AWS-2023-014]; *C.E. Wilson #s.n.*, [MMNS038015]; *C.E. Wilson Jr. #s.n.*, [ANHC008726]. **Prairie:** *T. Witsell #01-0621*, [ANHC005800]. **Randolph:** *Steimel #s.n.*, [AWS-2023-116]. **Woodruff:** *A.D. Ross & N.C. Chandler #s.n.*, [AWS-2025-017]. **CALIFORNIA. Butte:** *E. Dean et al. #850*, [UCR0020396] [DAV333755]; *J. DiTomaso #s.n.*, [DAV333754]; *L. Ahart #4810*, [MICH:1393521]; *W. Brim-DeForest #s.n.*, [DAV333778]. **Glenn:** *K. Duman #219*, [DAV338218]. DELAWARE. **Kent:** *K. Rash #s.n.*, [DOV0044971]. **Sussex:** *R.F. Naczi #8908*, [DOV0044969] [DOV0044970] [US:3477871]; *F.M. Uhler #s.n.*, [US:3605471]. FLORIDA. **Brevard:** *P.O. Schallert #s.n.*, [BRYV0068280]. **Duval:** *R.K. Godfrey #79160*, [BRIT246595] [FLAS:145743] [TTRS_000000320]. **Hillsborough:** *B. Upcavage #s.n.*, [FLAS:191135]; *B. Upcavage #s.n.*, [USF:201936]. **Seminole:** *P.O. Schallert #28277*, [BR0000021903250]. GEORGIA. **Chatham:** *E.O. Mellinger #1349*, [GAS009594]; *M.B. Mellinger #1587*, [GAS009520]. **Hall:** *R. Carter #8499*, [VSC0077942]. **Oglethorpe:** *F. Montgomery #710*, [GA013609]; *W. Duncan #3811*, [GA013608] [US:3155356]. **Richmond:** *A.E. Radford #45*, [NCSC00049738]; *A.W. Cusick #6561*, [BRIT246596]. **KENTUCKY. Ballard:** *R. Athey #3795*, [BRIT246597] [FSU:138717] [TENN-V-0039313]; *R. Cranfill #2805*, [BRIT246598]. **Calloway:** *R. Athey #3188*, [APSC0072305] [BRIT246599] [EKY:31234100076031] [TENN-V-0038836]. **Lyon:** *E.W. Chester #84-717*, [APSC0036021]. **Marshall:** *D.H. Webb #3660*, [FLAS:257192]; *D.H. Webb & W.M. Dennis #3660*, [BRIT246600] [FSU:138712] [TENN-V-0039314]; *R. Athey #3192*, [APSC0072304] [BRIT246601] [TENN-V-0038837] [TENN-V-0038943]. **Pike:** *F. Levy #s.n.*, [DUKE10041889]. **Trigg:** *D.H. Webb #7285*, [APSC0100982]; *E.W. Chester #84-590*, [APSC0036024]; *E.W. Chester #89-901*, [APSC0036022]; *J.W. Thieret #50785*, [BRIT246602] [KNK:31973000011236]. **LOUISIANA. Allen:** *C.M. Allen #11029*, [LSU00001487] [NLU0426290] [NLU0430043]; *R.D. Thomas #98125*, [NLU0426288]; *R.D. Thomas & C.M. Allen #98125*, [BRIT246603] [TENN-V-0039315]. **Avoyelles:** *W. McAtee #2216*, [US:588773]. **Caddo:** *J.V. Shireman #57*, [LSU00001488]. **Calcasieu:** *R. Carter #10532*, [BRIT246604] [FSU:138707] [IBE002743] [MICH:1393520] [VSC0045448] [US:3371216]. **Cameron:** *C. Reid #8964*, [LSU00139204] [VSC0067086]. **Catahoula:** *Hale #s.n.*, [US:875849]; *J. Hale #s.n.*,

[US:875848]; *J. Hale #s.n.*, [US:875850]. **East Baton Rouge:** *L. McKinney #9079*, [KNK:31973000011078]. **Iberia:** *H.P. Naquin II. #194*, [LSU00001490]. **Iberville:** *C. Reid & L.E. Urbatsch #7698*, [ANHC005801] [NCU00120005] [VSC0058506] [LSU00126082]; *C. Reid & L.E. Urbatsch #7699*, [LSU00127097]. **Jefferson Davis:** *C.A. Brown #9678*, [LSU00053354]. **Lafayette:** *A.J. Delahoussaye #SF6-9*, [DUKE10041891]. **LaSalle:** *C. Reid & S. Smith #7735*, [LSU00127064] [NCU00120001] [VSC0058507]; *C. Reid et al. #5294*, [LSU00098994] [LSU00099755] [LSU00099965]; *C. Reid et al. #5309*, [LSU00087531]; *C.E. DePoe #6845*, [NLU0430041]; *H.T. Hall #40*, [LSU00001492]; *J. Bruser #209*, [LSU00010384]; *J.D. Schroer #49*, [LSU00001491]; *K.E. Rogers #2541*, [NCU00192542]; *R.D. Thomas #17376*, [NLU0430040]; *R.D. Thomas #33186*, [NLU0426289]; *R.D. Thomas & K.E. Rogers #17376*, [BRIT246605] [NLU0430042]; *R.S. Cocks #s.n.*, [NO0033942]; *R.S. Campbell #RSC-224*, [US:3155354]; *N. Hotchkiss #5011*, [US:3605486] [US:3605485]. **Livingston:** *G.N. Montz #8327*, [SELU0011860]; *G.N. Montz #9292*, [SELU0011859]; *G.N. Montz & L. Fisher #6309*, [NO0033958] [SELU0011863]. **Rapides:** *J. Hale #s.n.*, [K002544102]. **St. Charles:** *K.S. Wiltenmuth #138*, [SELU0011869]. **St. Landry:** *C.M. Allen #17097*, [GSW:4537] [NLU0430039] [WILLI:57436]. **St. Tammany:** *B.E. Hebert #17*, [MISS0009289]; *B.E. Hebert #347*, [MISS0009290]; *B.E. Hebert #349*, [LSU00001494]; *E. Hebert #350*, [US:2974770]; *E. Hebert #348*, [US:2974771]. **Tangipahoa:** *F.M. Stouder #8*, [SELU0011861]; *G.N. Montz #7839*, [SELU0011865]; *S.L. Mayhew #36*, [SELU0011864]. **Vermilion:** *C.E. DePoe #6002*, [NLU0430037]; *J.W. Thieret #18302*, [PAC0076444]. **Vernon:** *J.W. Kessler #4996*, [BRIT246606]; *J.W. Kessler #5039*, [BRIT246608] [MICH:1393526]; *J.W. Kessler & R.D. Thomas #4996*, [MICH:1393527]; *R.D. Thomas #78060*, [NLU0430038]. **Uncertain:** *J.L. Webb #s.n.*, [US:693180]. **MARYLAND. Dorchester:** *W.D. Longbottom #10451*, [NY:2814402]. **Somerset:** *J. Trumbauer #s.n.*, [US:3363432]. **Wicomico:** *W.D. Longbottom #10138*, [NY:2814401]; *W.D. Longbottom #10324*, [NY:2814400]. **Worcester:** *J. Bright #1112*, [CM418885]; *J. Bright #1115*, [IND-0022955]; *W.D. Longbottom #12155*, [CM537969] [NY:2814399] [USF:267129] [US:3632646]; *W.D. Longbottom #13933*, [NY:2814398]. **MISSISSIPPI. Grenada:** *C.T. Bryson #23008*, [FLAS:281149] [MMNS036164] [SWSL001558] [VSC0003471]; *C.T. Bryson #23010*, [MMNS036165] [SWSL001559] [VSC0003470]; *C.T. Bryson #25523*, [APSC0126554] [VSC0080863] [USCH0073930] [MISSA036964]. **Harrison:** *C.T. Bryson #12815*, [BRIT246609] [NLU0430278] [SWSL001560] [TENN-V-0039316]; *C.T. Bryson #14284*, [SWSL001568]; *C.T. Bryson & R. Carter #13162*, [VSC0045449]; *C.T. Bryson & T.E. Newton #12815*, [IBE002744] [VSC0045450] [MISS0009287]. **Lafayette:** *T.M. Pullen #63193*, [MISS0008995] [MISS0009288] [USMS_000001005] [NCU00192543]. **Panola:** *C.T. Bryson #23016*, [FLAS:281151] [MMNS036162] [SWSL001561] [VSC0003468]. **Tishomingo:** *D.H. Webb & W.M. Dennis #3638*, [BRIT246610] [TENN-V-0039317]. **Washington:** *C.T. Bryson #16071*, [DOV0084286] [VSC0045457]. **Yalobusha:** *C.T. Bryson #s.n.*, [AWS-2022-BRYS]; *A.D. Ross & C.T. Bryson #s.n.*, [AWS-2025-GREN]; *A.D. Ross & C.T. Bryson #s.n.*, [AWS-2025-ENID]; *C.T. Bryson #28890*, [PIHG:18351] [USCH0079877]; *C.T. Bryson #22978*, [FLAS:281148] [MMNS036166] [SWSL001562] [VSC0003088]; *C.T. Bryson #23013*, [FLAS:281150] [MMNS036163] [SWSL001563] [SWSL001564] [VSC0003469]; *C.T. Bryson #23023*, [FLAS:281152] [MMNS036161] [SWSL001565] [VSC0003466]; *C.T. Bryson et al. #23642*, [MMNS036167]; *C.T. Bryson et al. #23644*, [MMNS036168]; *C.T. Bryson & N.B. Bryson #23636*, [FLAS:281153] [MMNS036169]; *C.T. Bryson et al. #23642*, [FLAS:281154]; *C.T. Bryson et al. #23644*, [FLAS:281155]. **MISSOURI. Butler:** *T. Butts #s.n.*, [AWS-2023-045]; *T. Butts #s.n.*, [AWS-2023-046]; *A. Ellis #s.n.*, [AWS-2023-120]. **Chariton:** *P.M. McKenzie #1878*, [ANHC008795] [VSC0045458]. **Pemiscot:** *J. Calhoun #s.n.*, [AWS-2023-029]. **Stoddard:** *S. Hudson #372*, [IND-0022956] [VSC0045459]. NEW MEXICO. **Hidalgo:** *K.D. Heil #33031*, [SJNM-V-0029187]; *R. Spellenberg & M. Spellenberg #6343*, [UNM0089561] [NY:2814428]; *R.D Worthington #15096*, [UNM0089562] [COLO:01067727] [DES00031010] [NY:2814410]; *R.D. Worthington #32254*, [ASU0099647] [SAT0053942]; *R.D. Worthington #36457*, [RSA0366780] [SRSC:19122]; *R.D. Worthington #32245*, [SAT0053896]; *L.N. Goodding #s.n.*, [US:1729097]. **Uncertain:** *C. Wright #1965*, [US:31983] [K002544100] [NY:2814437]. **NEW YORK. Nassau:** *W.C. Ferguson #4607*, [NY:2819737] [NY:2819738] [NY:2814405]. **NORTH CAROLINA. Beaufort:** *A.E. Blair #1046*, [NCSC00049293]; *A.E. Blair #25*, [NCSC00049294]; *A.E. Radford #36125*, [NCU00187715] [USF:15563]. **Bertie:** *F.H. Sargent #s.n.*, [BRYV0081686]; *H.E. Ahles & J.G. Haesloop #52107*, [NCU00187716]; *F.H. Sargent #70*, [US:2066981]. **Caswell:** *M.S. Reed & J.F. Reed #s.n.*, [DUKE10040727]. **Chatham:** *D.J. Drapalik #197*, [GAS025289]; *G.S. Ramseur & A.E. Hammond #2382*, [GA116438]; *G.S. Ramseur & A.E. Hammond #2879*, [NCU00187717]; *J. Tate #136*, [UNCC_50810]; *M. Sears #1431*, [UNCC_05842]; *M.F. Hanchey #152-51*, [DUKE10040728]; *S. Pritchard et al. #37*, [DUKE10040730]; *W.Wagamon & M. Zuckerberg #1*, [DUKE10040729]. **Craven:** *A.E. Radford #37355*, [FSU:138718] [NCU00187718]; *T. Bradley & B. Sears #3493*, [PAC0076445] [VSC0045451]; *T. Bradley et al. #3493*, [AUA000021314] [APSC0036020] [APSC0072281] [BOON:6869] [CONV0005682] [ECUH0002052] [FUGR0001907] [NBYC016489] [PEMB0001427] [UNCC_02290] [WCUH0010006] [WILLI:4467] [MISS0009291]; *T. Bradley, Sears & Bannister #3493*, [US:3620975]; *T.H. Kearney #2212*, [US:356868]; *T.H. Kearney #1969*, [US:356623]. **Cumberland:** *J.E. Benedict Jr. #3074*, [BRIT246611]; *R.L. Mears #401*, [EKY:31234100076049]; *Radford & Stewart #s.n.*, [NCU00187719]. **Currituck:** *J.C. Rabb #s.n.*, [NCSC00049295]. **Davidson:** *H.E. Ahles & R.S. Leisner #18681*, [NCU00187720]. **Duplin:** *R.L. Wilbur #59776*, [DUKE10040756]. **Durham:** *A. McDonald & A. Yellin #7*, [DUKE10040742]; *C.M. Taylor #1706*, [DUKE10040735]; *D.H.B. Ulmer Jr. #827*, [BRIT246612] [BRIT246613]; *D.O. Burge #306*, [DUKE10040755]; *D.S. Correll #8565*, [IND-0022959]; *F.R. Fosberg #17682*, [NCSC00049296] [RSA0365421]; *G.C. Tucker #1597*, [DUKE10040732]; *H.E. Ahles & M. Sears #59934*, [NCU00187722]; *H.L. Blomquist #5524*, [DUKE10040746]; *H.L. Blomquist #5526*, [DUKE10040751]; *H.L. Blomquist #7203*, [DUKE10040752]; *H.L. Blomquist #7204*, [DUKE10040741] [DUKE10040749]; *H.L. Blomquist #7205*, [DUKE10040750]; *M. Pyne #89-050*, [NCSC00049287]; *M.G. Stites #s.n.*, [NCU00187721]; *M.S. Reed #s.n.*, [DUKE10040745]; *M.S. Reed #s.n.*, [MUHW005858]; *M.S. Reed & J.F. Reed #s.n.*, [DUKE10040743]; *M.S. Reed & J.F. Reed #s.n.*, [DUKE10040744]; *M.S. Reed & J.F. Reed #s.n.*, [DUKE10040747]; *M.S. Reed & J.F. Reed #s.n.*, [DUKE10040748]; *M.S. Reed & J.F. Reed #s.n.*, [DUKE10040753]; *M.S. Reed & J.F. Reed #s.n.*, [DUKE10040754]; *M.S. Reed & J.F. Reed #s.n.*, [FLAS:11159]; *M.S. Reed & J.F. Reed #s.n.*, [GA116437]; *M.S. Reed & J.F. Reed #s.n.*, [IND-0022958]; *M.S. Reed & J.F. Reed #s.n.*, [RSA0366799]; *M.S. Reed & J.F. Reed #s.n.*, [WVA-V-0004127]; *R.L. Wilbur #33715*, [DUKE10040731]; *R.L. Wilbur #45019*, [DUKE10040733]; *R.L. Wilbur #49656*, [DUKE10040740]; *R.L. Wilbur #50377*, [DUKE10040737]; *R.L. Wilbur #57975*, [DUKE10040739]; *R.L. Wilbur #61647*, [DUKE10040734]; *R.L. Wilbur #86685*, [DUKE10040736]; *H. Blomquist #29*, [US:1568361]; *H. Blomquist #444*, [US:1568420]. **Edgecombe:** *A.E. Radford #38753*, [NCU00187723]. **Franklin:** *A.E. Radford #44310*, [USCH0061305] [NCU00187724] [UNCC_50811] [P01709068]; *H.L. Blomquist #13263*, [DUKE10040757]. **Gates:** *H.E. Ahles & J.A. Duke #48319*, [NCU00187725]. **Granville:** *H.E. Ahles & R.S. Leisner #17488*, [NCU00187726] [WVA-V-0004126]; *H.E. Ahles & R.S. Leisner #17513*, [NCU00187728]; *J.F. Reed & M.G. Stites #88*, [NCU00187727]; *J. Slapcinsky & L. Kelley #415*, [NCSC00049289]; *M.S. Reed & J.F. Reed #s.n.*, [DUKE10040758]; *M.S. Reed & J.F. Reed #s.n.*, [DUKE10040763]; *M.S. Reed & J.F. Reed #s.n.*, [NCU00187729]; *R.K. Godfrey #s.n.*, [NCSC00049290]; *R.L. Wilbur #42769*, [DUKE10040759]; *R.L. Wilbur #71901*, [DUKE10040760]; *R.L. Wilbur #71935*, [DUKE10040761]; *W.T. Batson Jr. #498*, [DUKE10040762]. **Greene:** *A.E. Radford #36495*, [FLAS:77486]; *A.E. Radford #36590*, [BRIT246614] [NCU00187730]. **Guilford:** *C.S. Parker #961*, [HUDC00000470] [HUDC00000471]. **Harnett:** *B.A. Sorrie #11394*,

[NCU00074007]; *Correll #2538*, [DUKE10040764]; *H. Laing #327*, [NCU00187731]; *R.K. Godfrey & W.B. Fox #49431*, [NCSC00049292]. **Hoke:** *L. Mitchell #s.n.*, [NCU00187732]; *R.L. Wilbur #61066*, [DUKE10040765]. **Johnston:** *A.E. Radford #27908*, [NCU00187733] [SIU017189]; *A.E. Radford #29188*, [RSA0365422]. **Jones:** *A.E. Radford #40032*, [NCU00187734]. **Lee:** *S. Stewart #s.n.*, [BR0000021903243]; *L.S. Beard #146*, [NCU00187738]. **Lenoir:** *A.E. Radford #28844*, [NCU00187735]. **Martin:** *A.E. Radford #39484*, [NCU00187736]. **Mecklenburg:** *J.F. Matthews #s.n.*, [UNCC_07280]. **Moore:** *H.J. Oosting #34788*, [DUKE10040766]. **Nash:** *H.E. Ahles & R.S. Leisner #21126*, [NCU00187737]. **New Hanover:** *G. McCarthy #s.n.*, [US:31924]. **Northampton:** *H.E. Ahles & J.A. Duke #45604*, [NCU00187739]. **Orange:** *A.E. Radford #332a*, [NCU00187741]; *H.L. Blomquist #5525*, [DUKE10040767]; *M.C. Coher #27*, [FSU:138721] [NCU00187740]; *M.S. Reed & J.F. Reed #s.n.*, [DUKE10040768]; *M.S. Reed & J.F. Reed #s.n.*, [USCH0061304]; *s.c. #15*, [NCU00187743]; *s.c. #16*, [NCU00187742]. **Pender:** *R.L. Wilbur #54302*, [DUKE10040769]. **Person:** *C.R. Bell #14663*, [K002544099] [GAS025575] [NCU00187745] [TENN-V-0039318] [IND-0022960]; *G. Crichton & D. Soo #104*, [DUKE10040771]; *G. Crichton & D. Soo #133*, [DUKE10040772]; *H.L. Blomquist #7202*, [DUKE10040773]; *H.L. Blomquist #7230*, [BRIT246615]; *J.A. Duke #0565*, [NCU00187744]; *M.S. Reed & J.F. Reed #s.n.*, [DUKE10040770]. **Pitt:** *A.E. Radford #39694*, [NCU00187746]. **Rowan:** *B.A. Sorrie #12021*, [NCU00099152]. **Scotland:** *D. Sharp #2117*, [NCU00187747]; *H.E. Ahles #36930*, [NCU00187748]. **Stokes:** *A.E. Radford #37799*, [NCU00187750]; *A.E. Radford #41282*, [NCU00187749]. **Tyrrell:** *A.E. Radford #39195*, [NCU00187751]. **Union:** *H.E. Ahles & J. Haesloop #31414*, [NCU00187752]. **Vance:** *H.E. Ahles #17300*, [MICH:1393528]; *H.E. Ahles & R.S. Leisner #17300*, [NCU00187753]; *M.S. Reed & J.F. Reed #s.n.*, [DUKE10040774]; *M.S. Reed & J. Reed #s.n.*, [US:1698750]. **Wake:** *H.H. Iltis #3710*, [NCSC00049297] [US:3155355]; *H.L. Blomquist #7201*, [DUKE10040778]; *L.F. Yelverton #s.n.*, [VSC0003684]; *R.L. Wilbur #43841*, [DUKE10040775]; *R.L. Wilbur #44801*, [DUKE10040777]; *R.L. Wilbur #45321*, [DUKE10040776]; *R.L. Wilbur #45414*, [DUKE10040784]; *R.L. Wilbur #57969*, [DUKE10040783]; *R.L. Wilbur #61689*, [DUKE10040782]; *R.L. Wilbur #69441*, [DUKE10040780]; *R.L. Wilbur & M. Alford #72046*, [DUKE10040779]; *R.L. Wilbur & M. Alford #72061*, [DUKE10040781]; *S.K. Ittenbach #464*, [NCSC00049388]; *H. Blomquist #10439*, [US:3155353]. **Washington:** *A.E. Radford #38826*, [NCU00187755]; *A.E. Radford #42455*, [NCU00187754]. **Wayne:** *C.J. Burk #23-11*, [NCU00187756]. **Wilkes:** *R.M. Downs #12427RMD*, [NCSC00049298]. **Wilson:** *A.E. Radford #37944*, [NCU00187757]; *H.L. Blomquist #6569*, [DUKE10040787]; *R.L. Wilbur #59988*, [DUKE10040786]; *R.L. Wilbur #60015*, [DUKE10040785]. **Uncertain:** *G. McCarthy #s.n.*, [USF:23880]; *G. McCarthy #s.n.*, [US:152159]; *G. McCarthy #s.n.*, [US:259419]; *G. McCarthy #s.n.*, [US:31925]; *McCarthy #s.n.*, [US:31923]; *G. McCarthy #s.n.*, [US:3159882]; *A. Michaux #s.n.*, [P00667331]; *G. McCarthy #249*, [US:818279]. **OHIO. Butler:** *Frank #s.n.*, [P01704448]. **SOUTH CAROLINA. Anderson:** *J.F. Townsend #1974*, [CLEMS0008110] [NBYC016357]. **Berkeley:** *H.W. Ravenel #s.n.*, [PBRU00010305]; *V.E. McNeilus #00-1141*, [BRIT246607] [TENN-V-0039319] [USF:271957]. **Charleston:** *H.E. Ahles & R.S. Leisner #32153*, [NCU00191539]; *J.M.M. Dougal #1471*, [DUKE10041887]; *J.M.M. Dougal #183*, [DUKE10041888]. **Cherokee:** *G. Newberry #1916*, [USCS0001465]; *H.E. Ahles & J.G. Haesloop #30920*, [NCU00191540]. **Chester:** *C.N. Horn #8777*, [NBYC016358]. **Clarendon:** *A.E. Radford #28061*, [NCU00191541]; *G. Long & M. Kiszner #701*, [USCH0089863]. **Colleton:** *V. McNeilus #94-852*, [TENN-V-0039320]. **Darlington:** *M.A. Curtis #s.n.*, [K002544101]; *M.A. Curtis #s.n.*, [NCSC00049687]; *M.A. Curtis #s.n.*, [P01704447]; *M.A. Curtis #s.n.*, [PBRU00010306]. **Dillon:** *H.E. Ahles & J.G. Haesloop #37175*, [NCU00191542]. **Fairfield:** *C.N. Horn #8712*, [CLEMS0006359] [MMNS075288] [NBYC016359]. **Florence:** *H.H. Bartlett #2344*, [MICH:1393524]. **Georgetown:** *C.P. Alexander #199*, [US:910438]. **Greenville:** *W.T. Batson #s.n.*, [FUGR0001928]. **Jasper:** *Carter & O'Brien #s.n.*, [GEO:14041]. **Kershaw:** *C.N. Horn & J. Bouknight #7645*, [CLEMS0006360] [NBYC016360]. **Lee:** *A.E. Radford #27295*, [NCU00191543]. **Lexington:** *A.E. Radford #27065*, [COLO:1067719] [NCU00191544]. **Marlboro:** *A.E. Radford #15474*, [NCU00191545]. **McCormick:** *A.E. Radford #30668*, [NCU00191546]. **Newberry:** *C.N. Horn #1379*, [GA116436] [NBYC016361] [UNCC_21020] [USCH0089862]; *C.N. Horn #13456*, [NBYC016356]; *C.N. Horn #17477*, [MU:000302700] [UVMVT299527]; *C.N. Horn & H. Scott #14891*, [DOV0084288]; *O.M. Freeman #56634*, [NCU00191548]. **Pickens:** *C.L. Rodgers & G. Shiflet, Jr. #69746*, [NCU00192140]; *H.D. House #2933*, [US:585365]. **Richland:** *O. Henry #597-1*, [USCH0089861]. **Saluda:** *A.E. Radford #30467*, [NCU00191547]; *C.N. Horn & H. Scott #14896*, [NBYC016355]. **Spartanburg:** *G. Newberg #7243*, [USCS0001467]; *R. Clark & C.G. Childress #19650*, [FUGR0001906]. **Union:** *G. Newberry #7426*, [USCS0001466]. **Uncertain:** *H. Ravenel #s.n.*, [HWR-0004019]. **TENNESSEE. Benton:** *D.H. Webb #6901*, [APSC0041107] [TENN-V-0038060]; *D.H. Webb #6926*, [TENN-V-0038058]; *D.H. Webb #7569*, [TENN-V-0038059]; *D.H. Webb & W.M. Dennis #3676*, [BRIT163214] [TENN-V-0038061]. **Cocke:** *D.H. Webb #s.n.*, [APSC0133348]; *D.H. Webb #s.n.*, [TENN-V-0255950]. **Davidson:** *N.H. Woodruff #s.n.*, [TENN-V-0038062]. **Decatur:** *D.H. Webb #7841*, [APSC0039858] [TENN-V-0243494]; *D.H. Webb et al. #1608b*, [TENN-V-0038063]. **Hamilton:** *D.H. Webb & D. Murphy #3687*, [BRIT163213] [TENN-V-0038064]. **Hardin:** *D.H. Webb #7890*, [APSC0041541] [TENN-V-0038065]. **Henry:** *D.H. Webb & B. Webb #3594*, [FLAS:257191] [FSU:138714] [TENN-V-0038066] [BRIT163211]. **Humphreys:** *D.H. Webb #6899*, [APSC0041109] [TENN-V-0038069]; *D.H. Webb #7559*, [APSC0036011] [TENN-V-0038068]; *D.H. Webb et al. #1772*, [BRIT163210] [TENN-V-0038070]; *R. Kral #54163*, [TENN-V-0038067] [VSC0045452] [BRIT163209]. **Jackson:** *D.H. Webb & D. Murphy #3506*, [FSU:138716]. **Jefferson:** *D.H. Webb & L. Bates #4742*, [BRIT163208] [FSU:138709] [TENN-V-0038071]. **Meigs:** *D.H. Webb & D. Murphy #3699*, [BRIT163207] [TENN-V-0038073]; *D.H. Webb & D. Murphy #3705*, [FLAS:257193] [FSU:138711] [TENN-V-0038072]. **Perry:** *D.H. Webb & B.S. Webb #1809*, [BOON:6868] [BRIT163206] [TENN-V-0038074]. **Shelby:** *C.T. Bryson & N.B. Bryson #13020*, [SWSL001566] [MICH:1393523] [VSC0045453]; *C.T. Bryson #13117*, [BRIT163205] [VSC0045454]. **Stewart:** *E.W. Chester #82-788*, [APSC0036019]; *E.W. Chester #83-466*, [APSC0036018]; *E.W. Chester #85-1036*, [APSC0036026]; *E.W. Chester #85-1059*, [APSC0036025]; *E.W. Chester #85-1138*, [APSC0036027]; *E.W. Chester #85-950*, [APSC0036017]; *E.W. Chester #90-449*, [APSC0036016]; *J. Joyner #601*, [APSC0036013]; *J. Joyner et al. #397*, [APSC0036015]; *J. Stack et al. #1062*, [APSC0036023] [APSC0036028] [NCU00192544]. **Wayne:** *D.H. Webb #7499*, [APSC0036012] [TENN-V-0038076]; *D.H. Webb #7617*, [APSC0039857] [TENN-V-0038075]. **TEXAS. Brazoria:** *J.W. Kessler #3742*, [BRIT246616]. **Fort Bend:** *S.D. Jones & R. Griffin #9678*, [DOV0084287] [PAUH:00012775] [SWSL001567] [MICH:1393532] [SAT0023348] [SAT0035133] [VSC0045455]. **Harris:** *J. Reverchon #3575*, [US:501059]. **Jeff Davis:** *B.H. Warnock #20098*, [TEX00288931] [FSU:138720]. **Jefferson:** *B. Higinbotham #7*, [US:3156657]. **Orange:** *S.D. Jones & G. Jones #10312*, [TENN-V-0039321] [VSC0045456] [MICH:1393522] [SAT0010800] [SAT0030430] [SAT0037354]. **Presidio:** *L.C. Hinckley #2840*, [NY:2814432]. **Walker:** *E. Keith #s.n.*, [BRIT483101]. **Wharton:** *S.M. Tracy #7698*, [NY:2814406]. **Uncertain:** *S.B. Buckley #s.n.*, [NY:2814414]; *S.B. Buckley #s.n.*, [NY:2814425]. **VIRGINIA. Accomack:** *S. Wine & A.M. Harvill #3035*, [FARM-0003540]; *T. Bradley #16304*, [GMUF-0014463]. **Brunswick:** *Barbara J. & A.M. Harvill #22528*, [FARM-0003711]. **Charlotte:** *G.P. Fleming & T. Wieboldt #14345*, [GMUF-0014465] [VPI-V-0028611]. **Chesapeake City:** *B. Mikula #3624*, [WILLI:20584] [FARM-0003538]; *B. Mikula #3654*, [WILLI:20833] [GMUF-0014459]; *G.P. Fleming & B. Carmean #12054*, [GMUF-0014457]; *R. Simpson #s.n.*, [LFCC-0002414]; *M.L. Fernald & L. Griscom #2782*, [USF:23881] [URV020214]; *R. Kral #13935*, [BRIT246620] [VPI-V-0028627]; *T.H. Kearney #1691*, [US:356358]. **Chesterfield:** *Barbara J. & A.M. Harvill*

#35904, [FARM-0003533]; *Barbara J. & A.M. Harvill #41221*, [FARM-0003712]; *R.A.S. Wright #1890*, [VCU-0013603]; *V. Guevara #s.n.*, [VCU-0013594]; *W.J. Hayden #2234*, [URV020215]; *W.J. Hayden #2529*, [URV020213]. **Dinwiddie:** *Aquatic Plants Class #48*, [VPI-V-0028628]; *R. Kral #11288*, [BRIT246617] [NCU00192546]. **Greensville:** *M.L. Fernald & B. Long #9544*, [FARM-0003539] [VPI-V-0028626]; *R. Kral #13850*, [BRIT246618] [FSU:138719]; *M.L. Fernald & B. Long #9542*, [P00254377] [US:1810091]. **Halifax:** *C.E. Stevens #23963*, [FARM-0003713]; *G.P. Fleming #14386*, [GMUF-0014466] [VPI-V-0028612]. **Henrico:** *Barbara J. & A.M. Harvill #40317*, [FARM-0003536]; *W.J. Hayden #2586*, [LYN-0012162] [URV020216]; *W.J. Hayden #2587*, [URV020212]. **Isle of Wight:** *L.L. Whitmarsh #613*, [WILLI:37280]. **King William:** *T. Bradley & D. Miller #18684*, [GMUF-0014461] [GMUF-0014462]. **Mecklenburg:** *Allen Belden Jr. #1651*, [GMUF-0014467]; *G.P. Fleming #14339*, [VPI-V-0028613]; *G.P. Fleming & T. Wieboldt #14339*, [GMUF-0014464]; *T. Wieboldt #9849*, [MICH:1393525]; *T.F. Wieboldt & G.P. Fleming #9849*, [VPI-V-0028610]. **New Kent:** *B. Mikula #3167*, [NLU0430277]; *B. Mikula #4479*, [WILLI:81047]; *A. Hollick & N.L. Britton #s.n.*, [NY:2814404]. **Northampton:** *S. Walker #16*, [NCU00261648]. **Nottoway:** *M.S. Rosenzweig #s.n.*, [VPI-V-0028629]; *Barbara J. & A.M. Harvill #40287*, [FARM-0003537]. **Southampton:** *A.M. Harvill #29493*, [FARM-0003541]; *B. Mikula #7399*, [LYN-0012163]; *B. Mikula #7702*, [VPI-V-0028630] [WILLI:14164]; *B. Mikula #7899*, [GMUF-0014458] [WILLI:14309]; *B. Mikula #8039*, [WILLI:14322]. **Stafford:** *H.H. Iltis #2309*, [CLEMS0008399] [FLAS:64113] [FLAS:64114] [GA116441] [LSU00070540] [MICH:1393519] [TENN-V-0039322] [USF:45969] [WILLI:10303] [US:02146981] [US:2054856] [US:1863203]; *H. O'Neill #2448*, [US:3099810]. **Suffolk City:** *A. Hollick & N.L. Britton #s.n.*, [SIM0009850]; *M.L. Fernald & B. Long #9543*, [CINC-V-0030537] [DUKE10041886] [MUHW005859]; *M.L. Fernald & B. Long #9545*, [US:1810092]; *R. Kral #11083*, [BRIT246619] [NCU00192545]. **Surry:** *F.R. Fosberg #17570*, [US:3499827]; *F.H. Sargent #194*, [US:2067066]. **Sussex:** *A.M. Harvill #22966*, [FARM-0003542]; *B. Mikula #3461*, [GMUF-0014460] [WILLI:20585]; *B. Mikula #3464*, [LYN-0012164]; *G.P. Fleming #8755*, [GMUF-0014456]; *R. Kral #11378*, [BRIT246621] [NCU00192547]. **Virginia Beach City:** *R.C. Simpson #s.n.*, [LFCC-0002298]; *R.C. Simpson #s.n.*, [LFCC-0008771]. **UNCERTAIN. Uncertain:** *Elliott #s.n.*, [K002544103]; *L. Wilkinson #s.n.*, [NCU00237160]; *s.c. #s.n.*, [NY:2814429].

APPENDIX 2
Global Specimens

Appendix 2 contains a list of global materials examined from outside of the United States of America, organized mostly by country but further by province/state for Australia, Brazil, India, Mexico, and Ecuador. All materials listed were examined by the authors; as such, the customary "!" notation is not included in citations. An abbreviated citation format has been chosen for reasons of practicality; enough information is present that any particular specimen can be easily found using the given institution barcode through its relevant data portal. The collections are formatted as follows: **COUNTRY. State/Province/Territory.** *Name #Number,* [Institution Barcode 1] [Institution Barcode 2] [etc.]. Unique collection events are separated by semicolons, and the last entry for any particular region ends with a period. When state locality information were not present or unclear on the label for any given sheet, they are listed under "Uncertain" within their respective country. A large portion of collections bore only handwritten labels; we apologize for any mistakes of transliteration. If any content was truly obscured, this is denoted in curly brackets as "*{obscured}*."

ANGOLA. *O.J.A. de Menezes #942*, [K002543267] [P01887232]. **ARGENTINA.** *A. Schinini et al. #17581*, [K002544437]; *A. Lefebvre #s.n.*, [BR0000021903298]. **AUSTRALIA. Northern Territory.** *P. Martens #AE817*, [K002454993]; *H.S. McKee #8337*, [K002454995]; *McKee #8337*, [P01820573]; *I.B. Wilson #242*, [K002454999]; *G. Chippendale #5487*, [K002454992]; *C. Dunlop #4505*, [K002454998]; *C. Dunlop #3467*, [K002454994]; *S.T. Blake #17575*, [K002454991]; *F. Mueller #s.n.*, [MEL247992]; *J. McKinlay #s.n.*, [MEL247991]; *K.L. Wilson #5036*, [NSW213535]; *K.L. Wilson #5014*, [NSW213536]; *K.L. Wilson #5031*, [NSW213537]; *K.L. Wilson & R.M. Barker #4941*, [NSW213529]; *K.L. Wilson #5242*, [NSW213527]; *P.N. Martensz #AE817*, [NSW213534]; *P.K. Latz #3451*, [NSW213530]; *P.K. Latz #1480*, [NSW213533] [NT31456]. **Queensland.** *T.A. Halliday #417*, [K002454984]; *J.R. Clarkson #132*, [K002454989] [NSW698438]; *S.T. Blake #13694*, [K002454985] [US:3167678]; *S.T. Blake #9009*, [K002454986]; *E.J. Thompson #BUC426*, [K002454990]; *S.T. Blake #9198*, [K002454987]; *S.T. Blake #13372*, [K002454988] [NSW698439] [NSW698437]; *B.S. Wannan #5473*, [NSW835807]; *I.D. Fox & G.W. Wilson #IDF3950*, [NSW842046] [BRI AQ0769945]; *E.J. Thompson & M. Edginton #LAW182*, [NSW824902] [BRI AQ0726272]; *I.D. Fox et al. #IDF3452*, [NSW841260] [BRI AQ0614892]; *K.R. McDonald #KRM3757*, [NSW837203] [BRI AQ0579748]; *B.S. Wannan & P. Graham #2827*, [NSW623780]; *E.J. Thompson & B.K. Simon #BUC426*, [NSW698436] [BRI AQ0542954]; *B.R. Jackes #s.n.*, [NSW213523]; *V.J. Neldner & T.D. Stanley #2465*, [NSW213526] [BRI AQ0433486]; *K.L. Wilson #5547*, [NSW213525]. **Western Australia.** *F.J.H. von Mueller #s.n.*, [K000881556]; *W.V. Fitzgerald #22635*, [US:2126637] [K002454997] [NSW22635]; *K.L. Wilson #4836*, [K002454996] [NSW698445]; *S. van Leeuwen #443*, [NSW815772] [PERTH 8222126]; *S. van Leeuwen #435*, [NSW815757] [PERTH 8222193]; *A.A. Mitchell #7066*, [NSW698440] [PERTH 6195687]; *A.A. Mitchell #3864*, [NSW698442] [PERTH 4381068]; *G. Graham #34*, [NSW698441]; *R.J. Cranfield #6360*, [NSW698443] [PERTH 2180804]; *S.W.L. Jacobs #5639*, [NSW223109]; *S.W.L. Jacobs & P.G. Wilson #5574*, [NSW698446]; *S.W.L. Jacobs & P.G. Wilson #5618*, [NSW223108]; *K.L. Wilson #4842*, [NSW213514]; *K.L. Wilson #4877*, [NSW213516]; *K.L. Wilson #4896*, [NSW213512]; *S.W.L. Jacobs #4297*, [NSW213518]; *K. Brennan #s.n.*, [NSW62500]; *K. Brennan #Spec4*, [NSW213517]; *D.E. Symon #10292*, [NSW698444] [BRI AQ0479047]; *H. Basedow #s.n.*, [NSW65201]; *H.J. Basedow #s.n.*, [NSW213519]; *W.V. Fitzgerald #s.n.*, [NSW65200]. **Uncertain.** *M. Lazarides #7840*, [K002455000]. **BENIN.** *L. Pauwels #7425*, [BR0000021151439]; *B. Sinsin #3603*, [MO-4362679]. **BOLIVIA.** *J.R. Abbott & B. Mostacedo #16145*, [VSC0045460]; *H.H. Rusby #1625*, [US:1230778]. **BOTSWANA.** *A. Heath & R. Heath #2637*, [K002543253]; *P.A. Smith #4410*, [K002543235] [BR0000018189117]; *P.A. Smith #1564*, [K002543266]; *P.A. Smith #1523*, [K002543233]; *J. Terry et al. #229*, [K002543260]; *P.A. Smith #3326*, [K002543257]; *R.P. Ellis #2728*, [K002543234] [P01710798]; *P.A. Smith #1940*, [K002543263]; *P.A. Smith #2421*, [K002543256]; *Alison & R. Heath #405*, [K002543261]; *P.A. Smith #1913*, [K002543258]; *P.A. Smith #1909*, [K002543265]; *Alison & R. Heath #929*, [K002543232]; *D.G. Long & D.A.H. Rae #539*, [K002543254]; *P.A. Smith #519*, [K002543236]; *G. Pope #385*, [K002543262] [P01887203]; *O.J. Hansen #3344*, [K002543255]; *P.A. Smith #2086*, [P01887202]. **BRAZIL. Amazonas.** *Martius #18885,* [W0337678]. **Bahia.** *F. França et al. #2228*, [FLOR0046854]; *L.R. Noblick #3758*, [JPB0029918]. **Ceará.** *J.R. Swallen #4496*, [US:1592180]; *D. Araújo & J.T.B. Jorge #1408*, [HVASF7780]; *L.R.O. Normando et al. #327*, [EAC0047834]; *P. Luetzelburg #26718*, [EAC0036556]; *S. Albuquerque #s.n.*, [EAC0001847]; *P. Luetzelburg #26729*, [EAC0036056] [FLOR0064362]; *E.B. Souza et al. #3256*, [EAC0058686]; *F. Freire-Allemão #s.n.*, [R010099352]; *P. Martins #s.n.*, [EAC0010128]; *P. Luetzelburg #26728*, [EAC0036554]. **Goiás.** *D. Butruille #s.n.*, [VIC:10322]. **Maranhão.** *G. Eiten & L.T. Eiten #3749*, [US:2688281] [INPA:249165] [K001174714]. **Minas Gerais.** *C.P. Cove et al. #958*, [R010099351]. **Pará.** *J.R. Swallen #6982B*, [US:1857283]; *I. Falesi #6*, [IAN111818]; *G.A. Black & P. Ledoux #50-10891*, [IAN062180]; *G.A. Black et al. #52-14359*, [IAN074087]. PARAÍBA. *V.M. Cotarelli et al. #1100*, [HVASF7781]; *P. Luetzelburg #28017*, [EAC0036053]; *P. Luetzelburg #27034*, [EAC0036557]; *J.A. Siqueira-Filho #2237*, [HVASF7778]; *V.M. Cotarelli et al. #2555*, [FLOR0065009]; *A.C.P. Oliveira et al. #2554*, [HVASF7566]; *A.C. Rodrigues et al. #44*, [JPB0034523]; *I.B. Lima et al. #575*, [JPB0037004]. **Paraná.** *R.C. Best #55a*, [INPA:111714]. **Pernambuco.** *B. Pickel #2452*, [US:1499838] [US:3202063]; *G.S. Baracho & J.A. Siqueira-Filho #339*, [HVASF7777]; *G. Fotius #3832*, [FLOR0064455]; *J.A. Siqueira-Filho et al. #2146*, [HVASF7779]. **Piauí.** *G. Gardner #2384*, [K000189209]; *L. Emperaire #s.n.*, [K000189210]; *L. Emperaire #2355*, [P06867659]. **Rio Grande do Norte.** *J.R. Swallen #4701*, [US:1592192]; *A.A. Roque #2942*, [RN00002108]; *s.c. #s.n.*, [RN00006987]; *A.R.O. Ribeiro & A.M.S. Araújo #144*, [EAC0045186]; *J.V.A. Medeiros #584*, [RN00009021] [HUEFS:293013]; *J.V.A. Medeiros #157*, [RN00007740]; *J.V.A. Medeiros #183*, [RN00007792]; *A.A. Roque #2941*, [RN00002107]; *A.A. Roque #2888*, [RN00002103]; *M.D. Melo #s.n.*, [RN00003763]. **Rio Grande do Sul.** *S.M. Hefler et al. #632*, [ICN00029452]; *V.G. Menezes #s.n.*, [FLOR0072208]; *S.M. Hefler #692*, [ICN00029450]; *S.M. Hefler et al. #438*, [ICN00029451]. **Sergipe.** *A.P. Prata #1607*, [FLOR0055351]; *M. Ibrahim et al. #18*, [FLOR0055160]. **Tocantins.** *G. Hatschbach et al. #60417*, [MBM164532]; *G. Pereira-Silva & G.A. Moreira #12472*, [CEN:00068051]. **Uncertain.** *Burchell #8567*, [K001174715]. **BURKINA FASO.** *A. Nongonierma #80*, [IFAN31955]; *B. Toutain & D. Dulieu #3098*, [P01887168]; *P.A. Schäfer #6284*, [P01887163]; *B. Toutain #2824*, [P01711326]; *B.M. Descoings & P.A. Schäfer #21846*, [P01887164]; *C. Bille #3290*, [P01887162]; *B. Toutain #101*, [P01887160]; *B. Toutain #1177*, [P01887169]; *C. Bille #2904bis*, [P01887161]; *J.G. Adam #15385*, [P01887159]; *B.M. Descoings & P.A. Schäfer #22271*, [P00584680]; *J. Sihvonen #167*, [US:2789247]. **BURUNDI.** *M. Reekmans #7711*, [K002540983] [BR0000025578089V] [BR0000018189674]; *M. Reekmans #2952*, [BR0000018189650]; *M. Reekmans #3467*, [BR0000018189667]; *J. Lewalle #1816*, [K002540987] [BR0000018189636] [BR0000025368505V]; *M. Reekmans #4337*, [BR0000018189681]; *M. Reekmans #4570*, [BR0000018189698] [P01887233]; *M. Reekmans #4305*, [BR0000018189643]. **CAMEROON.** *A. Meurillon #1385*, [K002540988]; *F.J. Breteler #410*, [K002540986] [BR0000018188790]; *W.J.J.O. de Wilde & B.E.E. Duyfjes #3224*, [K002540985]; *E. Bounougou #34*, [K002540989]; *R. Letouzey #6283*, [BR0000018188783] [P01887175]; *E. Bounougou #34*, [BR0000018188776] [P01887182]; *W.J.J.O. de*

Wilde & B.E.E. De Wilde-Duyfjes #3196, [BR0000018188820]; *H. Jacques-Félix #8351*, [BR0000018188806]; *s.c. #7385*, [BR0000018188813]; *W. de Wilde & B.E.E. de Wilde-Duyfjes #3224*, [BR0000018188844] [P01887173]; *W.J.J.O. de Wilde et al. #5021*, [BR0000018188837]; *J. Raynal & A. Raynal #12718*, [P01887180] [P01887181] [P01734135]; *R. Letouzey #6283bis*, [P01887176] [P01710802]; *R. Letouzey #68{obscured}6*, [P01887177]; *W.J.J.O. de Wilde #3196*, [P01887174]; *A.P.M van der Zon #1283*, [P01887187]; *H. Jacques-Félix #8351*, [P01887170]; *N. Boubée #45H*, [P01887179]; *B. Mbélé & D. Klein #927*, [P01887184]; *A. Gaston #3252*, [P01887171]; *R. Letouzey #5801*, [P01887183]; *A. Vaillant #402bis*, [P01887172]; *A. Meurillon #1385*, [P01887165]; *W. de Wilde #5021bis*, [P01887167]. **CENTRAL AFRICAN REPUBLIC.** *J.M. Fay #2821*, [K002540980]; *J.M. Fay #2976*, [K002540981]; *J.M. Fay #3394*, [K002540979]; *C. Tisserant #1976*, [P01887218] [BR0000018188875] [BR0000018188899]; *G. Le Testu #3014*, [BR0000018188851] [BR0000018188905] [P01887217]; *C. Tisserant #2172*, [BR0000018188868] [BR0000018188882] [P01887064]; *A. Chevalier #7963*, [P01887219]; *C. Tisserant #3554*, [P01887073] [P01887215] [P01887072]; *C. Tisserant #2888*, [P01887220] [P01887078]. **CHAD.** *Audru #704*, [P06867680] [P01710799] [P01734136] [P01710800] [P01887235]; *G. Fotius #832*, [P01887236] [P01887240]; *A.B.G. & J. Audru #287*, [P01887248]; *P. Palayer #338*, [P01887249]; *J. Audru #322*, [P01887063] [P01887066]; *Audru #592*, [P01710801] [P01887234]; *Audru #1809*, [P01887230]; *A. Gaston #2009*, [P01887241] [P01734168]; *J. Audru #325*, [P01887238]; *A. Chevalier #8969bis*, [P01887229]; *A. Gaston #2122*, [P01734134]; *Audru #944*, [P01887231]; *J. Koechlin #4827*, [P01887239]; *A. Gaston #1930*, [P01887242]; *B.P. de Fabrègues #3016*, [P01887237]; *A. Chevalier #7709*, [P01887065]; *H. Gillet #s.n.*, [P00958653]. **COLOMBIA.** *J. Betancur & M. Berrio #2004*, [US:3253341]. **COSTA RICA.** *G. Davidse & R.W. Pohl #1325*, [US:3054605]. **CÔTE D'IVOIRE.** *Audru #5580*, [P01887188]; *C. Geerling & J. Bokdam #2571*, [BR0000018188714]. **DEMOCRATIC REPUBLIC OF THE CONGO.** *Fasseaux #1236*, [K002540998]; *Fasseaux #1093*, [K002540999]; *A. Noirfalise #738*, [K002540996] [K002540993]; *De Kimpe #7*, [K002540992] [BR0000018189469]; *Fasseaux #1235*, [K002540997]; *L. Pauwels #6217*, [BR0000018189230]; *J. Symoens #11977*, [BR0000025378429V] [BR0000025378436V] [BR0000018189483] [K002540991]; *A. Schmitz #6697*, [BR0000018189452]; *H. Vanderyst #s.n.*, [BR0000018189254]; *H. Vanderyst #1308*, [BR0000018189278]; *H. Vanderyst #1309*, [BR0000018189285]; *H. Vanderyst #2226*, [BR0000018189292] [BR0000018189261]; *H. Vanderyst #2456*, [BR0000018189315]; *H. Vanderyst #2521*, [BR0000018189308] [BR0000018189322]; *H. Vanderyst #4220*, [K002540990]; *A.M. De Graer #s.n.*, [BR0000018189377]; *F. Hens #392A*, [BR0000018189162]; *G. Troupin #1829*, [K002540994] [BR0000018189391]; *G. Troupin #1664*, [BR0000018189421]; *L. Pauwels #4352*, [BR0000018189223]; *J. Symoens #12453*, [BR0000025368512V]; *J. Claessens #1632*, [BR0000018189186]; *H. Brédo #2637*, [BR0000018189346]; *L. Pauwels #5396*, [BR0000018189247]; *F. Hens #358*, [BR0000018189353] [P01887226] [K002540995]; *J. Loumaye #72*, [BR0000018189445]; *G. Troupin #1290*, [BR0000018189407]; *G. Troupin #738*, [BR0000018189384]; *R.G.A. Germain #6098*, [BR0000018189438]; *F. Hens #392B*, [BR0000018189179]; *J. Bequaert #7484*, [BR0000018189193]; *L. Pauwels #4685*, [BR0000018189216]; *G. Troupin #1589*, [BR0000018189414]; *H. Brédo #2217*, [BR0000018189476]; *J. Bequaert #7210*, [BR0000018189209]; *F. Hens #392*, [P01887225]. **ECUADOR.** *E. Asplund #5155*, [R010099353] [US:1930421]; *E. Asplund #15604*, [R010099354]; *E. Asplund #s.n.*, [K002544421]; *E. Asplund #s.n.*, [K002544420]; *Spruce #6417*, [K002544422]; *H.K. Svenson #11425*, [US:183826]. **Galápagos Province** *A. Stewart #1039*, [US:920973]. **ESWATINI.** *C. Parker #1076*, [K002543942]. **ETHIOPIA.** *Schimper #1199*, [K000363004] [MO-1515488] [US:3648063] [MPU028211] [TUB-007254] [TUB-007255] [TUB-007256] [TUB-007267] [TUB-007268] [HEID-701327] [HOH-009006] [HOH-009007] [P01887228] [P01834986] [P01887221] [P01887223] [P01887222] [US:945558] [BR0000008452429]; *Schimper #1551*, [K000363005] [US:945721]; *I. Friis et al. #13611*, [BR0000015245991V]; *I. Friis et al. #11845*, [K002541272]; *I. Friis et al. #7257*, [BR0000018188929]; *L.R. Quartin-Dillon #s.n.*, [P01887224]. **GABON.** *C.M. Wilks #W99,* [EIU018609]. **GEORGIA.** *P.W. Massalsky #s.n.*, [K002453791]; *G. Woronow #s.n.*, [K002453792]; *K. Koch #s.n.*, [B 10 0296611]; *K. Koch #1700*, [B 10 0296610]; *G.J.N. Woronow #619*, [GZU000012876]; *G.J.N. Woronow #618*, [GZU000012877]; *G.J.N. Woronow #620*, [GZU000012874] [GZU000012875]. **GHANA.** *J.B. Hall #3143*, [K002540494] [P01711331]; *J.B. Hall #2070*, [K002540488]; *J.B. Hall #V B S 1269*, [K002540489]; *J.B. Hall #cc388*, [K002540486]; *J.B. Hall #cc582*, [K002540487]; *J.B. Hall #GC39605*, [P01711337]; *J.B. Hall #582*, [P01711328]. **GUINEA.** *Dinter #7528*, [K002543946] [K002543945]; *J. Chillon #2421*, [P01711333]; *C.-H. Pobéguin #398*, [P01711335] [P00584648]; *J.G. Adam #14801*, [P01711329]; *J. Chillon #2704*, [P01711336]; *C.-H. Pobéguin #1062*, [P01711334]. **GUINEA-BISSAU.** *J.A. Pereira #3280,* [MA-01-00274057]. **HONDURAS.** *J. Escobar #1-A,* [MO-3772920]. **INDIA. Karnataka.** *V.P. Prasad #172932*, [BSI0000111468] [BSI0000111473]; *V.P. Prasad #173825*, [BSI0000111469] [BSI0000111472]; *V.P. Prasad #173732*, [BSI0000111470] [BSI0000111471]; *S.S. Hooper & K.N. Gandhi #HFP 2421*, [K002454498]; *T. Cooke #s.n.*, [K002454495]. **Kerala.** *J. Stocks #s.n.*, [K000592585] [P01714704] [P01714705]; *W.-K. Veucoba-Rao #3650*, [K002454500]. **Maharashtra.** *V.D. Vartak #10740*, [K002454496]; *s.c. #s.n.*, [K002454497]; *R.R. Fernandez #R7334*, [K002454499]. **Uncertain.** *J.O. Voigt #504*, [US:2126822]. **KENYA.** *D.M. Napper & O. Mwangangi #2011*, [K002542164]; *M.G. Gilbert & M. Thulin #1710 A*, [K002542163]; *A. Bogdan #AB 4961*, [K002542167]; *S.S. Hooper & C.C. Townsend #1183*, [K002542169]; *P.A. Luke & Q. Luke #5728*, [K002542161]; *P.A. Luke & Q. Luke #5631*, [K002542166]; *J. McMahon #K236*, [US:2892921]. **MADAGASCAR.** *S. Andriambololonera et al. #410*, [K001991463] [P00820425]; *R. Decary #443*, [K002543572] [K002543567] [P01875717]; *G.F.S. Elliot #2189*, [K002543569]; *J. Blackburn & A. Bowles #s.n.*, [K002543575]; *J. Blackburn & A. Bowles #s.n.*, [K002543573]; *R. Baron #4258*, [K002543571] [P01875714] [P01875712]; *Bojer #s.n.*, [K002543568]; *R. Decary #390*, [K002543570] [P01875724]; *J.V. Thomson #104A*, [BR0000018189131]; *S.E. Rakotoarisoa & M. Andriamahay #SNGF3340*, [P02171658]; *S.E. Rakotoarisoa & M. Andriamahay #SNGF3353*, [P02171680]; *R. Decary #s.n.*, [P01701194]; *E.-G. Waterlot #783*, [P01875701]; *P. de la Bâthie #2497*, [P01875710]; *P. de la Bâthie #13111*, [P01875718] [P01875719] [P01875697]; *P. de la Bâthie #930*, [P01875722]; *P. Boiteau #325-20*, [P01875729] [P01880400]; *R. Decary #1698*, [P01875706]; *R. Decary #430*, [P01875725]; *R. Decary #1687*, [P01875698] [P01875733] [P01875734]; *P. Boiteau #325-10*, [P01880402]; *L. Rotereau #s.n.*, [P01708765]; *s.c. #102*, [P01875703]; *s.c. #325-27*, [P01875728] [P01880399]; *R. Decary #16499*, [P01875700]; *P. Boiteau #1318*, [P01875702]; *E.G. Waterlot #283*, [P01875715] [US:1505110]; *R. Portères #s.n.*, [P01916090]; *E.G. Waterlot #280*, [P01875716]; *P. de la Bâthie #1056*, [P01875720]; *s.c. #325-10*, [P01875727]; *A. Grandidier #s.n.*, [P01880401]; *M. Catat #75*, [P01875705]; *s.c. #3580*, [P01875731]; *R. Decary #1699*, [P01875707] [P01875704]; *P. de la Bâthie #2452*, [P01875709]; *P. de la Bâthie #2496*, [P01875708] [P01875711]; *P. de la Bâthie #14204*, [US:3200514] [P01875732] [P01875730]; *s.c. #s.n.*, [P01875713]; *R. Decary #397*, [P01875721]; *L.M.A. du Petit-Thouars #s.n.*, [P00459829] [P00459830]. **MALAWI.** *A. Whyte #s.n.*, [K002543187]; *A. Whyte #s.n.*, [K002543188]; *A.B. Cormack #219*, [K002543185]; *G. Jackson #1450*, [K002543186] [BR0000018189070] [BR0000018189063]; *A.J. Salubeni #1548*, [K002543183]; *C.O. Dudley #1626*, [K002543184]; *A.B. Cormack #s.n.*, [K002543189]. **MALI.** *J. Davey #085*, [K002540480]; *P. Jaeger #18*, [K002540482]; *J. Davey #070*, [K002540483]; *O. Hagerup #429*, [BR0000018188691]; *C. de Wailly #4887*, [P01711352]; *Bondet #A00H1-41*, [P01711341]; *s.c. #2471*, [P01711342]; *F. Barlet #24*, [P01734012]; *M. Alassane #13732*, [P01711355]; *s.c. #54bis*, [P01734123] [P01711351]; *A. Chevalier #1090*,

[K002540490] [P01887077]; *A. Chevalier #2473*, [BR0000018188707] [P01711339]; *s.c. #2474*, [P01711340]; *A. Chevalier #2484*, [K002540481] [P01711338]; *J. Raynal #5031*, [P01711354]; *A. Chevalier #43818*, [P01711343]; *A.B. #3493*, [P01711376]; *A. Chevalier #43790*, [P01711349]; *G. Boudet #5813*, [P01711348]; *De Wailly #4893*, [BR0000018188912] [P01711345]; *A. Chevalier #43092*, [P01711353]; *Rouget #s.n.*, [P01711344]; *M. Alassane #s.n.*, [P01710810]; *Mission d'études de la biologie des acridiens #235*, [P00869912]; *J. Raynal #5126*, [P01711358]. **MAURITANIA.** *J.G. Adam #21829-4*, [K002540468]; *D. Dupont #147*, [BR0000018188264]; *M. Carrière #300*, [P01734125]; *s.c. #s.n.*, [P01711359]; *D. Sadio #s.n.*, [P01711386]. **MAURITIUS.** *Sieber #7*, [K000363062] [P01870794] [P00459964]; *Grey #s.n.*, [K000363061]; *Maire #s.n.*, [P01870799]. **MEXICO. Baja California.** *J. Rebman #18679*, [SD00011283]; *E.A. Mearns #2282*, [US:233018]. **Chihuahua.** *C.G. Pringle #s.n.*, [DOV0084284]; *C.G. Pringle #s.n.*, [DOV0084285]; *C.G. Pringle #810*, [BR0000021903311] [MICH:1133793] [P00254381] [P00254382] [P00254379] [US:818324]. **Guanajuato.** *A. Dugés #s.n.*, [K002544223]; *A. Dugés #s.n.*, [P00578445]. **Guerrero.** *G.B. Hinton #9460*, [MICH:1133789] [US:1977957] [US:3167684] [K002544220]; *{obscured} Gil #22-C*, [US:3130938]. **Jalisco.** *A.A. Beetle #M-7069*, [MICH:1133783]; *C.L.D. Luna #12975*, [MICH:1133787]; *C. Feddema #99*, [MICH:1133792]; *G. Tucker #2995*, [MICH:1133774]; *L. González-Villarreal #625*, [MICH:1133786]; *L.M.V. de Puga #7682*, [MICH:1133795]; *R.L. Wilbur #36701*, [MICH:1133785]; *R.L. Wilbur #36761*, [MICH:1133770]; *R. McVaugh #17271*, [MICH:1133790]; *R. McVaugh #18575*, [MICH:1133780]; *R. McVaugh, C. Feddema & R.W. Pippen #18575*, [US:2451653]; *R. McVaugh #20007*, [MICH:1133781]; *H.H. Iltis #3258*, [MICH:1133784]. **State of Mexico.** *G.B.H. #4685*, [K002544218]; *G.B. Hinton #4685*, [US:1636240] [US:3167685]; *E. Bourgeau #528*, [P00254309] [P00254308]. **Michoacán.** *N.D. Luna #s.n.*, [MICH:1133794]; *T.R. Soderstrom #565*, [MICH:1133796] [US:2396068]; *G. Arsène #3174*, [K002544219] [BR0000021903335] [P00578453] [P00254307] [US:1032151] [MBM294317]; *G. Arsène #5643*, [K002544217] [P00254306] [US:1032857]; *J. Rzedowski #49992*, [BR0000021903304]; *G. Arsène #643*, [P00578452]; *G. Arsène #s.n.*, [P00578447]; *G. Arsène #2401*, [US:1032780]; *G. Arsène #7317*, [US:1032240]. NAYARIT. *C. Feddema #1326*, [MICH:1133782]; *C. Feddema #552*, [MICH:1133775]; *C. Feddema #564A*, [MICH:1133791]; *F.W. Pennell #19887*, [US:1642096] [US:3167683]. **Oaxaca.** *G. Tucker #2911*, [MICH:1133773]; *R.L. Wilbur #36549*, [MICH:1133772]; *R.L. Wilbur #36567*, [MICH:1133771]; *R.M. King & C. Feddema #1768*, [US:2363532]. SAN LUIS POTOSÍ. *Virlet #1182*, [P00254305]. SONORA. *S.L. Friedman & J.D. Freeh #297*, [ASU0006230]; *T. Van Devender et al. #95-800*, [USON:9198]; *I.L. Wiggins & R.C. Rollins #275*, [MICH:1133776] [US:1892840]. VERACRUZ. *s.c. #s.n.*, [P00254310]. **MOZAMBIQUE.** *J. Buchanan #62*, [K002543190]; *H.B. Gilliland #Q1828*, [K002543181]; *J.G. Pedro #4560*, [BR0000018189100]. **MYANMAR.** *Scott #s.n.*, [P01714703]. **NAMIBIA.** *H. Giess #10047*, [K002543943]; *W. Giess #15238*, [K002543944]; *H. Merxmüller & W. Giess #2054*, [BR0000018189148]; *B. Strohbach & T. Sheuyange #BS3159*, [US:3626845]. **NICARAGUA.** *M. Nee #28331*, [BRIT647002]; *W.D. Stevens #9989*, [P01786999]. **NIGER.** *E. Boudouresque #H5619*, [K002540470]; *Boudouresque #H5626*, [K002540473]; *Boudouresque #H5606*, [K002540471]; *E. Boudouresque #H5621*, [K002540472]; *G. Cremers #964*, [BR0000018188738] [P01887247]; *G. Cremers #949*, [P01887246] [BR0000018188745]; *E. Robbrecht #3327*, [BR0000018188721]; *N. Leman #29*, [BR0000018188752]; *B. Roussel #Niger 8*, [P01082319]; *s.c. #695*, [P01711350]; *J. Koechlin #6393*, [P01887157] [P01711332]; *M. Saadou & M. Garba #746*, [P01887186]; *B.P. de Fabrègues #2303*, [P01887244]; *J. Koechlin #6618*, [P01887158]; *B.P. de Fabrègues #1993*, [P01887067]; *B.P. de Fabrègues #2099*, [P01887245]; *M. Saadou #156*, [P01887250]; *G. Boudet #4930*, [P01887061]; *B.P. de Fabrègues #2883*, [P01887243]; *B.P. de Fabrègues #1993*, [P01887062]; *J.-F. Duranton #1302*, [P01887185]; *R. Portères #s.n.*, [P01194717]; *A. Marchal #s.n.*, [P00924954]. **NIGERIA.** *C.D.K. Cook #426*, [K002540511]; *J.D. Kennedy #8008*, [K002540508]; *D.W. Lawlor & J.B. Hall #559*, [K002540506]; *D.W. Lawlor & J.B. Hall #218*, [K002540510] [BR0000018188769]; *K.A. Kershaw #900348*, [K002540507]; *D.W. Lawlor & J.B. Hall #FHI 46539*, [K002540521]; *D.M. Gurts #120*, [K002540518]; *M.G. Latilo #FHI62586*, [K002540503]; *J.M. Dalziel #241*, [K002540514]; *D.W. Lawlor & J.B. Hall #15*, [K002540522]; *R. Wheeler Haines #212*, [K002540519]; *D.W. Lawlor & J.B. Hall #FHI 46537*, [K002540504]; *P. Wit & Fagbemi #1240*, [K002540474]; *W.H. Batten-Poole #402*, [K002540516]; *M.G. Latilo #62799*, [K002540523]; *D.W. Lawlor & J.B. Hall #384*, [K002540505]; *K.A. Kershaw #900690*, [K002540512]; *Johnston #55*, [K002540509] [K002540517]; *M.G. Latilo #62645*, [K002540520]; *J.L. Lowe #1530*, [K002540502]; *D.W. Lawlor & J.B. Hall #FHI 46538*, [K002540513]; *P. Wit et al. #s.n.*, [P01887166]. **PARAGUAY.** *Rojas #2286A*, [SI000242]; *Rojas #3112*, [US:3200933]. **PERU.** *S. McDaniel & M.Y. Rimachi #23344*, [BR0000021903328] [BRIT647004]; *M.Y. Rimachi #11100*, [VSC0045463]; *M.Y. Rimachi #8741*, [VSC0045461] [VSC0045462] [BRIT647003]; *M. Rimachi Y. #11100*, [US:3345611]; *R.A. Ferreyra, E. Cerrate & Ó. Tovar #10918*, [US:2282740]; *M. Rimachi Y. #8741*, [US:3260050]; *R.A. Ferreyra #9063*, [US:2282716]. **RWANDA.** *J. Raynal #20705*, [K002540982] [BR0000009255524] [P01887204]; *G. Troupin #15034*, [BR0000018189605]; *G. Troupin #15043*, [BR0000018189582]; *P. Van der Veken #9059*, [BR0000025578096V] [BR0000018189629]; *G. Bouxin & M. Radoux #INRS/175*, [BR0000018189513]; *G. Bouxin & M. Radoux #252b*, [BR0000018189490]; *G. Troupin #6943*, [BR0000018189551]; *P. Van der Veken #10818*, [BR0000018189612] [BR0000022441089]; *G. Troupin #6798*, [BR0000018189544]; *B. Runyinya #244*, [BR0000018189520]; *G. Troupin #8501*, [BR0000018189575]; *G. Troupin #8507*, [BR0000018189568]; *G. Troupin #14843*, [BR0000018189599]; *G. Bouxin & M. Radoux #INRS/43*, [BR0000018189506]. **SENEGAL.** *J.-P. Heudelot #537*, [P01711387] [P01711385] [P01711381] [P01710805] [K002540463] [BR0000018188288] [BR0000018188271]; *J.G. Adam #18577*, [K002540467] [P01711398]; *S. Laegaard et al. #16849*, [K002540462]; *Roger #20*, [K002540466]; *J.A. Broadbent #113*, [K002540464]; *F.N. Hepper #3612*, [K002540469]; *Roger #39*, [K002540465]; *C. Vanden Berghen #3356a*, [BR0000018188363]; *C. Vanden Berghen #3628*, [BR0000018188516]; *C. Vanden Berghen #6309*, [BR0000018188608]; *C. Vanden Berghen #2622a*, [BR0000018188417]; *J. Berhaut #505*, [BR0000018188301] [P01711371]; *J. Berhaut #2643*, [BR0000018188295] [P01711372]; *C. Vanden Berghen #6406b*, [BR0000018188653]; *C. Vanden Berghen #3653a*, [BR0000018188547]; *C. Vanden Berghen #3663*, [BR0000018188523]; *C. Vanden Berghen #6377*, [BR0000018188615]; *C. Vanden Berghen #10374*, [BR0000018188332]; *C. Vanden Berghen #3319b*, [BR0000018188431]; *G. Compaore #s.n.*, [BR0000018188684]; *C. Vanden Berghen #3301a*, [BR0000018188455]; *E. Faye #108*, [BR0000005098811]; *C. Vanden Berghen #3640*, [BR0000018188530]; *C. Vanden Berghen #2763*, [BR0000018188448]; *G. Perrottet #876*, [BR0000018188318]; *C. Vanden Berghen #2695a*, [BR0000018188400]; *C. Vanden Berghen #2530*, [BR0000018188394]; *C. Vanden Berghen #5986b*, [BR0000018188639]; *C. Vanden Berghen #8705*, [BR0000018188646]; *C. Vanden Berghen #7187a*, [BR0000018188677]; *F.R. Leprieur #s.n.*, [BR0000018188325] [P00573082] [P00573083]; *C. Vanden Berghen #7143a*, [BR0000018188660]; *D. Champluvier #S/116*, [BR0000018188349]; *C. Vanden Berghen #2483*, [BR0000018188387]; *C. Vanden Berghen #3366e*, [BR0000018188370]; *C. Vanden Berghen #2643a*, [BR0000018188424]; *C. Vanden Berghen #6374*, [BR0000018188622]; *C. Vanden Berghen #3659a*, [BR0000018188493]; *C. Vanden Berghen #3834c*, [BR0000018188561]; *C. Vanden Berghen #3345b*, [BR0000018188479]; *C. Vanden Berghen #3472*, [BR0000018188486]; *C. Vanden Berghen #6326*, [BR0000018188585]; *C. Vanden Berghen #3546*, [BR0000018188462]; *C. Vanden Berghen #3557b*, [BR0000018188509]; *C. Vanden Berghen #6039*, [BR0000018188554]; *C. Vanden Berghen #4902*, [BR0000018188578]; *C. Vanden Berghen*

#6050c, [BR0000018188592]; *C. Vanden Berghen #2576a*, [BR0000018188356]; *J. Trochain #284bis*, [P01711399] [P01711402]; *M. Huard #s.n.*, [P01711380]; *G.S. Perrotet #876*, [P01711378] [P01711379] [P01710807]; *C.R.A. Bambey #450*, [P01711368]; *J. Raynal & A. Raynal #6091*, [P01887070] [P01710806] [P01711405]; *A.K. Diallo #408*, [P01711388] [P01710809]; *J.-P. Heudelot #316*, [P01711383] [P01711382]; *J.C. Bille #3409*, [P01711360]; *G. Boudet #3514*, [P01711391]; *J. Berhaut #5557*, [P01711365]; *J.C. Bille #3410*, [P01711361]; *J. Raynal & A. Raynal #7609*, [P01711406] [P01710804] [P01710803]; *Richard #s.n.*, [P01711377]; *A.K. Diallo #391*, [P01711393]; *J.G. Adam #1921*, [P01711389]; *G. Boudet #3891*, [P01734011]; *J. Trochain #4960*, [P01711396]; *J.G. Adam #2060*, [P01711394]; *A.K. Diallo #391(246)*, [P01711375]; *Couey #15*, [P01711407]; *J. Trochain #2260*, [P01711395]; *J. Trochain #271*, [P01711404]; *J. Berhaut #2644*, [P01711367]; *J. Trochain #2009*, [P01711362]; *J.-P. Heudelot #317*, [P01711384]; *s.c. #49bis*, [P01711363]; *Gouvern. du Senegal #s.n.*, [P01711318]; *G. Boudet #3507*, [P01711392]; *G. Boudet #3662*, [P01711390]; *G. Boudet #3892*, [P01711373]; *G. Boudet #3493*, [P01711369]; *J. Adam #XI.51*, [P01711364]; *G. Boudet #3832*, [P01734133]; *s.c. #s.n.*, [P01710808]; *J. Trochain #4902*, [P01711400]; *Berhaut #2645*, [P01711366]; *A.K. Diallo #1045*, [P01734124] [P01711397]; *J. Trochain #303*, [P01711401]; *Maire #s.n.*, [P01711370]; *J. Trochain #307bis*, [P01711403]; *A.K. Diallo #408(263)*, [P01711374]; *Fotius #426*, [P01711357]; *H. Gillet #257*, [P00958782]; *S. Lægaard, J.E. Madsen & S. Traore #16849*, [US:3325894]. **SEYCHELLES.** *C.P. Bélanger #s.n.*, [P01714701]; *L.A. Deschamps #s.n.*, [P01714702]. **SIERRA LEONE.** *H.D. Jordan #464*, [K002540485]. **SOUTH AFRICA.** *R. Schlechter #4663*, [K002543947]; *R. Schlechter #12195*, [K002543182] [BR0000018189124] [P01887196]; *s.c. #s.n.*, [P01887068]; *F.A. Rogers #s.n.*, [K002543948]. **SOUTH SUDAN.** *J.H. Davies #s.n.*, [K002541270]; *A. Peney #s.n.*, [P01887212]; *G. Schweinfurth #{obscured}*, [P01887208]; *G. Schweinfurth #1939*, [P01887209]; *G. Schweinfurth #2018*, [P01887206] [K000363008] [S13-17825]. **SUDAN.** *G.E. Wickens #429*, [K002541268]; *G.E. Wickens #2499*, [K002541262]; *J.K. Jackson #2316*, [K002541269]; *F. Sillitoe #82*, [K002541265]; *N.D. Simpson #7573*, [K002541266]; *J.G. Myers #8599*, [K002541263]; *W.B. Ritchie #1*, [K002541267]; *J.M. Lock #81/156*, [K002541264]; *Kotschy #52*, [P01887213] [P01887214] [P01834989] [K000363006] [K000363007] [US:3648064] [US:806285] [US:02231894] [BR0000009860933] [TUB-007269] [HEID-701326] [HOH-009005]; *G. Schweinfurth #2012*, [P01887210] [P01887205]; *G. Schweinfurth #2029*, [P01887207]. **TANZANIA.** *S. Bidgood et al. #5285*, [K000190515] [BR0000005014026] [P01734126] [K002542183]; *Q.E. Haarer #815*, [K002542197]; *A. Bjørnstad #AB 1995*, [K002542182]; *S.S. Hooper et al. #2048*, [K002542179]; *H.A. Lindemann #276*, [K002542195]; *S.S. Hooper et al. #2049*, [K002542180]; *P.J. Greenway & R.M. Polhill #11648*, [K002542177]; *J.H. Vaughan #1862*, [K002542201] [K002542200]; *P.J. Greenway & Kanuri #13994*, [K002542186]; *L. Thomas #28*, [K002542171]; *R.L. Davis #216*, [K002542196] [PH00805547]; *G.C. de Nevers & S. Charnley #3323*, [K002542181]; *S.S. Hooper et al. #1946*, [K002542178]; *J. Mdehwa #20*, [K002542189]; *C. Pêtre #18*, [K002542174] [BR0000018188981]; *S.S. Hooper et al. #2028*, [K002542185]; *Evans #1137*, [K002542170]; *J.R. Zimmerman #7583*, [K002542193]; *E. Milne-Redhead & P.G. Taylor #9162*, [K002542175] [BR0000018188950] [P01887193]; *Boivin #s.n.*, [K002542202]; *L.H. Boivin #s.n.*, [BR0000018189025]; *Boivin #s.n.*, [P01887069]; *M. Thulin & B. Mhoro #769*, [K002542187]; *D.P. Pielou #136*, [K002542172] [BR0000018188974]; *A. Michelmore #1492*, [K002542194] [BR0000018188998]; *J.C. Lovett & C.J. Kayombo #4658*, [K002542176]; *G.A. Peter #44693*, [K002542198]; *Acres #119*, [K002542188]; *R. Polhill & S. Paulo #2163*, [K002542173] [P01887195]; *G.A. Peter #12143*, [K002542199]; *S.S. Hooper & C.C. Townsend #2049*, [BR0000018189032]; *R.M. Polhill & S.P. Kibuwa #2163*, [BR0000018188943]; *L. Van Meel #1137*, [BR0000018188967]; *C. Sacleux #1640*, [BR0000018189018] [P01887192]; *L. Van Meel #1209*, [BR0000018189001]; *P.J. Greenway #14165*, [P01887190]; *R.B. Drummond & J.H. Hemsley #3397*, [P01887191]; *M. Danschel #s.n.*, [P01834990]. **THE GAMBIA.** *P.J. Terry #1858*, [K002540478]; *Ruxton #118*, [K002540476]; *H. Macluskie #15*, [K001734124]; *B.O.L. Duke #10*, [K002540477]; *H. Macluskie #6*, [K002540475]; *J.P. Ruxton #87*, [K002540479]. **TOGO.** *U. Scholz et al. #090*, [K002540496]; *P. Hiepko & W. Schultze-Motel #216*, [K002540500] [P01711330]; *H. Ern et al. #1215*, [K002540495]; *H. Ern et al. #517*, [K002540499] [P01711327]; *U. Scholz et al. #269*, [K002540501]; *U. Scholz et al. #206*, [K002540497]; *U. Scholz et al. #013*, [K002540498]. **UGANDA.** *K.A. Lye & A. Katende #5435*, [K002542159]; *R.W. Haines #4193*, [K002542192] [P01887227]; *Ziegler #7*, [K002542156]; *I. Langdale-Brown #1243*, [K002542160]; *A.B. Katende #K 2256*, [K002542157]; *R. Dümmer #1017*, [K002542190]; *K.A. Lye & M. Namaganda #25209*, [K002542158]; *C. Kabuye #90*, [K002542191] [BR0000018188936]; *E.A. Mearns #2744*, [US:632734]. **VENEZUELA.** *J. Steyermark & M. Rabe #96488*, [US:2585313]. **ZAMBIA.** *W.L. Astle & S.D. Prince #470*, [K002543202]; *P.S.M. Phiri #2090*, [K002543200]; *H.M. Richards #15413*, [K002543206]; *H.J. Van Rensburg #1623*, [K002543194]; *H.M. Richards #15463*, [K002543201]; *H.M. Richards #5008*, [K002543197] [BR0000018189056]; *Richards #9006*, [K002543205]; *J.-J. Symoens #11493*, [K002543193]; *J. Kornas #3405*, [K002543198]; *Michelmore #409*, [K002543207]; *E.A. Robinson #491*, [K002543195]; *R.B. Drummond & R.O.B. Rutherford-Smith #7440*, [K002543199]; *S.A. Renvoize #5709B*, [K002543191]; *Michelmore #422*, [K002543208]; *Van Laviesen et al. #713*, [K002543196]; *E.A. Robinson #2132*, [K002543204]; *R.K. Brummitt et al. #14310*, [K002543192]; *P.J. Tyrer #224*, [BR0000018189049]; *H.M. Richards #12504*, [P01887194]. **ZIMBABWE.** *R.B. Drummond #5653*, [K002543220]; *J.B. Phipps #1014*, [K002543217] [K002543215]; *O.B. Miller #7885*, [K002543224] [K002543225] [P01887197]; *O.B. Miller #4295*, [K002543216] [BR0000018189155]; *H. Wild #1750*, [K002543230] [K002543229]; *E.G. Gibbs Russell #1561*, [K002543227]; *C.K. Brain #4528*, [K002543212] [BR0000018189087]; *Rattray #1236*, [K002543209]; *S. Mavi #973*, [K002543223] [P01887189]; *G.E. Gibbs Russell #1589*, [K002543231]; *C.K. Brain #8928*, [K002543213]; *C.K. Brain #8407*, [K002543210]; *C.K. Brain #8777*, [K002543214]; *H. Wild #5419*, [K002543221]; *R.B. Drummond #5382*, [K002543218] [BR0000018189094]; *C.K. Brain #8778*, [K002543226]; *C.K. Brain #8401*, [K002543211]; *Hornby #H2439*, [K002543222]; *K.A. Lye #23847*, [K002543219]; *G.E. Gibbs Russell #1628*, [P01887199]; *G.E. Gibbs Russell #1610*, [P01887201]. **Uncertain.** *P. Jaeger #5762*, [P01887076]; *J.G. Adam #15040*, [P01711347]; *s.c. #s.n.*, [P01887178]; *s.c. #526*, [P01711346]; *H. Gillet #s.n.*, [P00992978].

APPENDIX 3

Other Selected Reference Specimens

Appendix 3 contains a list of materials examined as part of the larger survey of African and South Asian *Pycreus* material selected by the authors to illustrate key points throughout this work. The abbreviated citations for the original type material of *C. macrostachyos* Lam. and *C. puncticulatus* Vahl have been included here. All materials listed were examined by the authors; as such, the customary "!" notation is not included in citations. General locality information is provided as in Appendices 1 and 2, and Indian collections are separated by state. The collections are organized by species and formatted as follows: **COUNTRY. State.** *Name #Number,* [Institution Barcode 1] [Institution Barcode 2] [etc.]. Collection events are separated by semicolons, and the last entry for any particular region ends with a period. When state locality information were not present or unclear on the label for any given sheet, they are listed under "Uncertain."

Cyperus macrostachyos Lam.—**UNCERTAIN ("Ex Africa" fide Lamarck 1791).** *s.c. #s.n.,* [P00668535]; *s.c. #s.n.,* [P00573081].

Cyperus puncticulatus Vahl—**INDIA. Tamil Nadu.** *K.M. Matthew #26276,* [K000496540]; *A.G. Bourne & L. Bourne #s.n.,* [K000496539]. **UNCERTAIN.** *s.c. #s.n.,* [C10010313]; *s.c. #s.n.,* [C10010314]. SRI LANKA. *Thwaites #3751,* [BR0000021904776] [P01714707]; *R.G. Cooray #70032311R,* [US:02225358].

Cyperus malaccensis Lam.—**MALAYSIA. Malacca.** *Sonnerat #52,* [P00587042].

Cyperus latifolius Poir.—**MADAGASCAR.** *L.M.A. du Petit-Thouars #s.n.,* [P00450595].

cf. *Cyperus filicinus* [?]—**UNITED STATES OF AMERICA. South Carolina.** *L.A.G. Bosc #s.n.,* [MPU028131].

Cyperus strigosus—**UNCERTAIN – NORTH AMERICA.** *Peck #s.n.,* [LINN-HS 104.21].

Cyperus pelophilus—**ANGOLA.** *F. Welwitsch #7025,* [LISU224778] [LISU224779] [BM000922522]; *F. Welwitsch #7080,* [MPU028172]; *F. Welwitsch #7082,* [LISU224781] [LISU224780] [LISU224784].

Cyperus longistolon (= *C. chrysanthus*)—**BOTSWANA.** *A. Heath & R. Heath #2048,* [K002542437]; *P.A. Smith #2994,* [K002543264]. **TANZANIA.** *P.J. Greenway #7778,* [K002541302]. **ZIMBABWE.** *F.A. Rogers #5090,* [K002543228]. **ZAMBIA.** *H.J. van Rensburg #1131,* [K002542422]. **UNCERTAIN.** Klaasen #EK262, [US:02231025].