ERIGERON BEYRICHII (ASTERACEAE), A NEW COMBINATION AND REDEFINITION OF A WIDESPREAD TAXON IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT

The *Erigeron annuus-E. strigosus* species complex is an assemblage of several generally narrowly distributed sexual diploid populations in the southeastern United States plus the widespread apomictic polyploid taxa *E. annuus* and *E. strigosus*. *Erigeron strigosus* var. *beyrichii* has previously been used to describe plants with diffuse branching and smaller capitula, and it has also been presumed to be polyploid and apomictic. An herbarium specimen at the University of Georgia (GA) was examined that is a duplicate of an original Beyrich collection made in "Carolina" in 1833 that was acquired and distributed by the British Museum (BM). Cotton blue in lactophenol stained pollen provides unambiguous evidence for the diploid and sexual condition of the specimen. Digital images of the putative type specimen of the taxon at LE as well as additional digital specimens from BM and HUH were also examined. The evidence supports the new combination **Erigeron beyrichii**. This is a sexual diploid species on the coastal plain of the United States in South Carolina, Georgia, Florida, and Alabama. The nomenclatural update brings the taxon into parallel status with other sexual diploid taxa that have recently been described in the complex.

RESUMEN

El complejo de especies *Erigeron annuus-E. strigosus* es un conjunto de varias poblaciones diploides de distribución sexual generalmente estrecha en el sudeste de Estados Unidos, además de los taxones apomícticos poliploides *E. annuus* y *E. strigosus*, muy extendidos. *Erigeron strigosus* var. *beyrichii* se ha utilizado anteriormente para describir plantas con ramificación difusa y capítulos más pequeños, y también se ha supuesto que es poliploide y apomíctica. Se examinó un espécimen de herbario de la Universidad de Georgia (GA) que es un duplicado de una colección original de Beyrich realizada en "Carolina" en 1833 que fue adquirida y distribuida por el Museo Británico (BM). El polen teñido con azul de algodón en lactofenol proporciona pruebas inequívocas de la condición diploide y sexual del espécimen. También se examinaron imágenes digitales del espécimen tipo putativo del taxón en LE, así como especímenes digitales adicionales de BM y HUH. Las pruebas apoyan la nueva combinación **Erigeron beyrichii.** Se trata de una especie diploide sexual de la llanura costera de Estados Unidos en Carolina del Sur, Georgia, Florida y Alabama. La actualización de la nomenclatura pone al taxón en paralelo con otros taxones diploides sexuales que se han descrito recientemente en el complejo.

INTRODUCTION

Apomictic complexes provide a daunting biosystematic challenge and a wealth of opportunities for studying evolutionary processes. Typically, they comprise widespread polyploid apomictic entities and narrowly distributed sexual diploid populations (Stebbins 1950). Presumably one or more of the sexual diploids in a complex are the progenitors of the apomictic polyploids. Recurrent origins and hybridization among constituent populations lead to complex patterns of variation. Nonetheless, one of the primary objectives taxonomically is to discover and describe the usually coherent sexual diploid components of apomictic complexes (Grant 1981). Classic studies in *Antennaria* (Bayer 1987; Bierzychudek 2012), *Amelanchier* (Burgess et al. 2014), and *Ranunculus* (Hörandl 2014), for instance, have led to the recognition of sexual diploid biodiversity and provided insight into the origin, ecology, reproductive biology, and evolution of apomictic complexes.

Erigeron annuus (L.) Pers. and *E. strigosus* Muhl. ex Willd. are both widespread annual to short-lived perennial herbaceous taxa in eastern North America with scattered distributions in western North America, with presumably recent introductions of *E. annuus* occurring in Central America, Europe, and Asia (Nesom 2006). Cronquist (1947) considered both taxa to be largely apomictic and accepted two and five

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morphological varieties, respectively, for the two species. Nesom (1989) included *E. annuus* and *E. strigosus* in a narrowly defined *E.* sect. *Phalacroloma* and noted that while all chromosome counts for *E. annuus* to that date had been triploid (and therefore likely apomictic), both triploid and diploid (presumably sexual) chromosome counts had been published for *E. strigosus*.

Subsequent field work, chromosome counts, and phylogenetic analyses have led to the recognition of two morphologically distinct sexual diploid ($2n = 18$) species in the southeastern United States: *E. allisonii* D.B. Poind., B.R. Keener, & Noyes (Weakley et al. 2018), which occurs on limestone glades in Middle Tennessee and adjacent Georgia and Alabama, and, *E. dolomiticola* (J. Allison) D.B. Poind., B.R. Keener, and Noyes (Weakley et al. 2017) which is restricted to dolomite outcrops in central Alabama. Further, analysis of pollen from > 2700 herbarium specimens for *E. strigosus* (Noyes & Allison 2005; Noyes 2007), in conjunction with developmental analysis and chromosome counts from field material, found that plants on the coastal plain of the Southeast, extending from South Carolina through Georgia to adjacent Alabama, and into northern Florida are commonly sexual and diploid. However, a biologically meaningful name for these plants has been wanting.

Nomenclatural History

Erigeron strigosus was originally described in 1803 from collections by Muhlenberg in Pennsylvania that were then incorporated into the Willdenow Herbarium at Berlin (Cronquist 1947). Given the northern latitude of the collection, the type specimen, presumably destroyed in WWII, is assumed to have been apomictic. Therefore, we conclude that the "*strigosus*' epithet is not biologically appropriate for the southern U.S. sexual diploid populations.

The Prussian botanist Heinrich Karl Beyrich collected plants in Georgia and adjacent "Carolina" in 1833/1834 (Brendel 1875; Geiser 1956) and appears to have sent multiple sets of his specimens to Europe, including to Berlin (B) where they were provisionally annotated, anonymously, as "*Erigeron beyrichii*" (Fischer & Meyer 1840). Seeds from Beyrich collections were grown at B and also LE and herbarium specimens from those garden plants then appear at LE (Cronquist 1947). The epithet "*beyrichii*' associated with these specimens first appears validly in the literature as the basionym *Stenactis beyrichii* Fisch. & C.A. Mey. in 1839 (name only), and then in 1840 as the combination *Phalacroloma beyrichii* (Fisch. & C.A. Mey.) Fisch. & C.A. Mey., with an accompanying description. The name then occurs at the varietal level as *E. strigosus* var. *beyrichii* (Fisch. & C.A. Mey.) A. Gray in 1884 with a short description. Cronquist (1947) accepts *Erigeron strigosus* var. *beyrichii* as one of five varieties of the species and presumes that the taxon is apomictic.

In the course of herbarium specimen pollen survey (Noyes 2007), an herbarium specimen (Fig. 1) from the University of Georgia, U.S.A. (GA) (accession #137802) was encountered that appears to be an original Beyrich collection. The specimen originated from the herbarium of the British Museum (BM), bears the Beyrich name, the collection number #180, and is dated 1836, close to the known time of Beyrich's collection trip to the southeastern U.S. in 1833. Cursory analysis showed that the specimen bears pollen consistent with the sexual diploid condition, and the specimen is morphologically consistent with sexual diploid plants that occur throughout the southeastern coastal plain.

The objectives of this study were to 1) document more thoroughly the pollen sample from the GA Beyrich specimen, and, 2) to explore the nomenclatural and type history of the "*beyrichii*" taxon to determine the suitability of the name for southeastern U.S. sexual diploid populations heretofore referred to as "sexual diploid *Erigeron strigosus*."

MATERIALS AND METHODS

Six florets at or near anthesis were removed from a capitulum of the (GA) herbarium sheet. Florets were soaked on a glass slide in excess cotton blue in lactophenol (Stanley & Linskens 1974) over a two-day period. Florets were then macerated with forceps to release pollen and most floral debris was removed. For this work, a pollen slide made in 2006 was restained with fresh cotton blue in lactophenol. Overall pollen quality was assessed as grains "viable" if they were uniformly and darkly stained blue or "nonviable" if they were clear

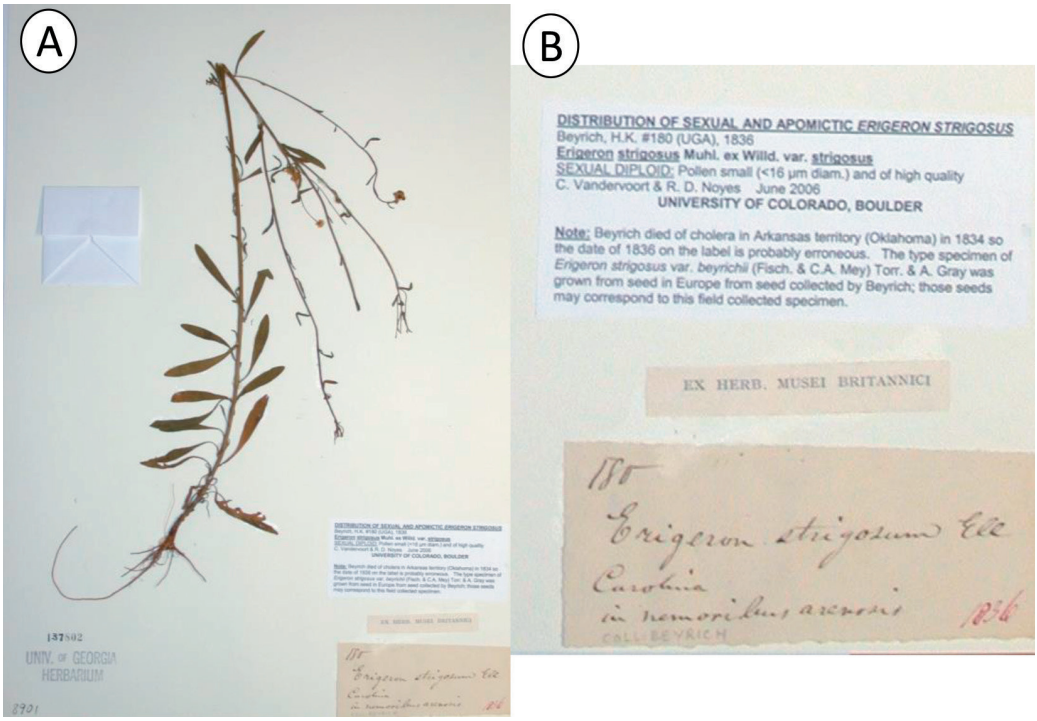

Fig. 1. GA accession #137802, *Beyrich 180*. A. Specimen showing narrow stem leaves and components of a diffuse branching system. B. Label details documenting *Beyrich 180* and collected in Carolina in 1836. The specimen was probably actually collected in 1833. Beyrich died in 1834, so the later date on the specimen is erroneous. A high resolution digital image may be accessed at http://oi.org/10.5281/zenodo.14743001.

(non-staining) or contained stained but shrunken cytoplasm within the grain wall. To document variation in size among putatively viable pollen grains, images of 300 staining grains were captured at 400× with Nomarski (Phase Contrast) optics, and grain diameter was estimated using AnalySIS (version 3.1) image-capturing and analysis software. Pollen diameters were plotted in histogram form in Microsoft Excel (2019) and the values were compared with measures from previous work (Noyes & Allison 2005).

Digital images of putative type and related historical herbarium specimens of the "*beyrichii*" taxon were obtained from BM, HUH, and LE for comparison with the GA specimen. Specimens were evaluated in light of the nomenclatural history in the published literature as well as accounts of Beyrich's collecting trip to the southeastern U.S. and the deposition of his collections.

RESULTS

Pollen Quality

The pollen quality estimated for the GA #137802 Beyrich specimen is unambiguously consistent with the sexual diploid condition. Pollen grain sizes average 13.97 µm diameter (standard deviation 0.80) (Fig. 2A), which is close to the average of 15.0 um (range 14.1 µm–16.3 µm, standard deviation 0.66) obtained for a survey of 40 known sexual diploids sampled of *E. strigosus* (Noyes & Allison 2005). In addition, pollen grains were almost entirely uniformly stained (Fig. 2B) with crenulate, non-staining grains exceedingly rare. This is in contrast to pollen samples for polyploid apomicts that feature larger grains and with a high percentage of abortive grains and therefore low stainability.

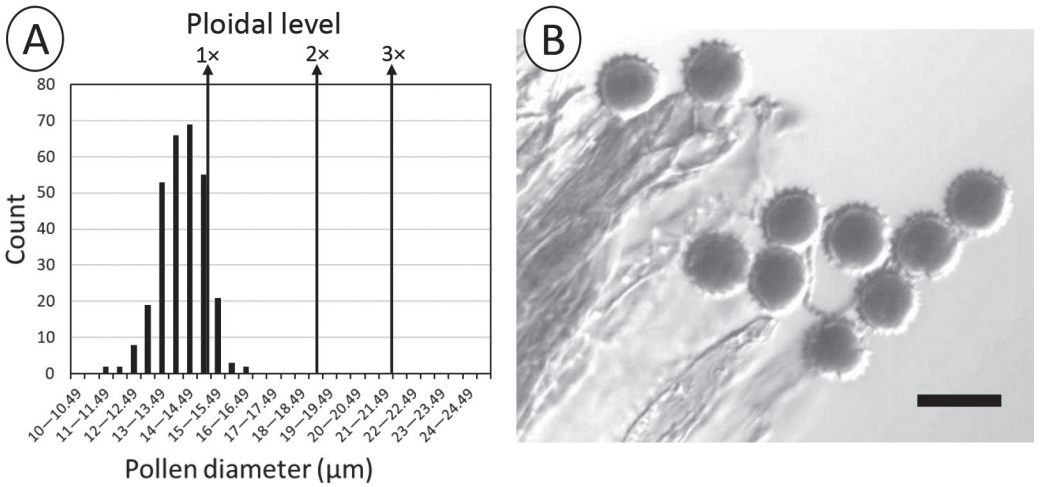

Fig 2. Analysis of pollen obtained from GA accession #137802, *Beyrich 180*. A. Histogram showing that pollen mean diameter is consistent with measures obtained for other diploid plants in the complex (Noyes & Allison 2005). B. Sample micrograph of pollen showing uniform staining in cotton blue in lactophenol and size. Scale bar = 20 µm.

Historical Specimens

Digital images of herbarium specimens were obtained from BM, HUH, and LE that are relevant to the nomenclatural history of the "beyrichii" taxon. High-resolution digital images of these specimens may be accessed at https://doi.org/10.5281/zenodo.14743001. The BM specimen (Fig. 3A) is of interest as its labels closely mirrors GA #137802 consistent with its duplicate status. Both the BM and the GA specimen show specimen #180, locality (Carolina) and habitat description (*in nemoribus arenosis*), and identification ("*Erigeron strigosum*") with similar handwriting and formatting. The GA specimen adds the collector as Beyrich, and the collection year as 1836. The BM specimen is insect-damaged but otherwise is similar to the GA specimen from which pollen was obtained. The BM herbarium sheet includes two additional collections, from Oregon, and Arkansas, apparently for comparative purposes. The BM sheet includes a yellow descriptive note (upper left) that is consistent with the Beyrich specimen having been purchased by BM as a component of the Shuttleworth Herbarium (Ranee Prakash, BM Curator, pers. comm.).

The HUH (Gray Herbarium) specimen (Fig. 3B) was prepared from garden plants by Asa Gray upon his visit to Berlin (B) in 1839. It features diffuse inflorescence branching, small heads, and short strigose pubescence consistent with the BM collection. The specimen presumably served as the reference specimen by Asa Gray for the combination *Erigeron strigosus* Muhl. ex Willd. var. *beyrichii* (Fisch. & C.A. Mey.) A. Gray in 1884. Cronquist notes on the specimen "The most nearly authentic specimen to be found in this country."

The LE specimens (Fig. 3C, D) were grown from seeds from an original Beyrich collection. The annotation of the first specimen (Fig. 3C) by Meyer indicates that the seed were obtained from the Herbarium at "Wratislaw," understood to refer to Wroclaw, Poland, to which Beyrich must have sent a set of specimens. The specimen is not dated but bears the name *Stenactis beyrichii*, which was published in 1839. The second specimen from LE (Fig. 3D), is labeled as *Phalacroloma beyrichii*, the combination having been made in 1840. The two specimens are robust, but similar in overall morphology to the GA, BM, and HUH specimens.

DISCUSSION

According to British Museum (Natural History) (1906), BM acquired the 170,000 specimen Shuttleworth Herbarium in 1877 that included a set of Beyrich specimens from North America. Shuttleworth, in turn, apparently acquired the Beyrich specimens via the purchase of the Roemer Herbarium at Zurich (JSTOR

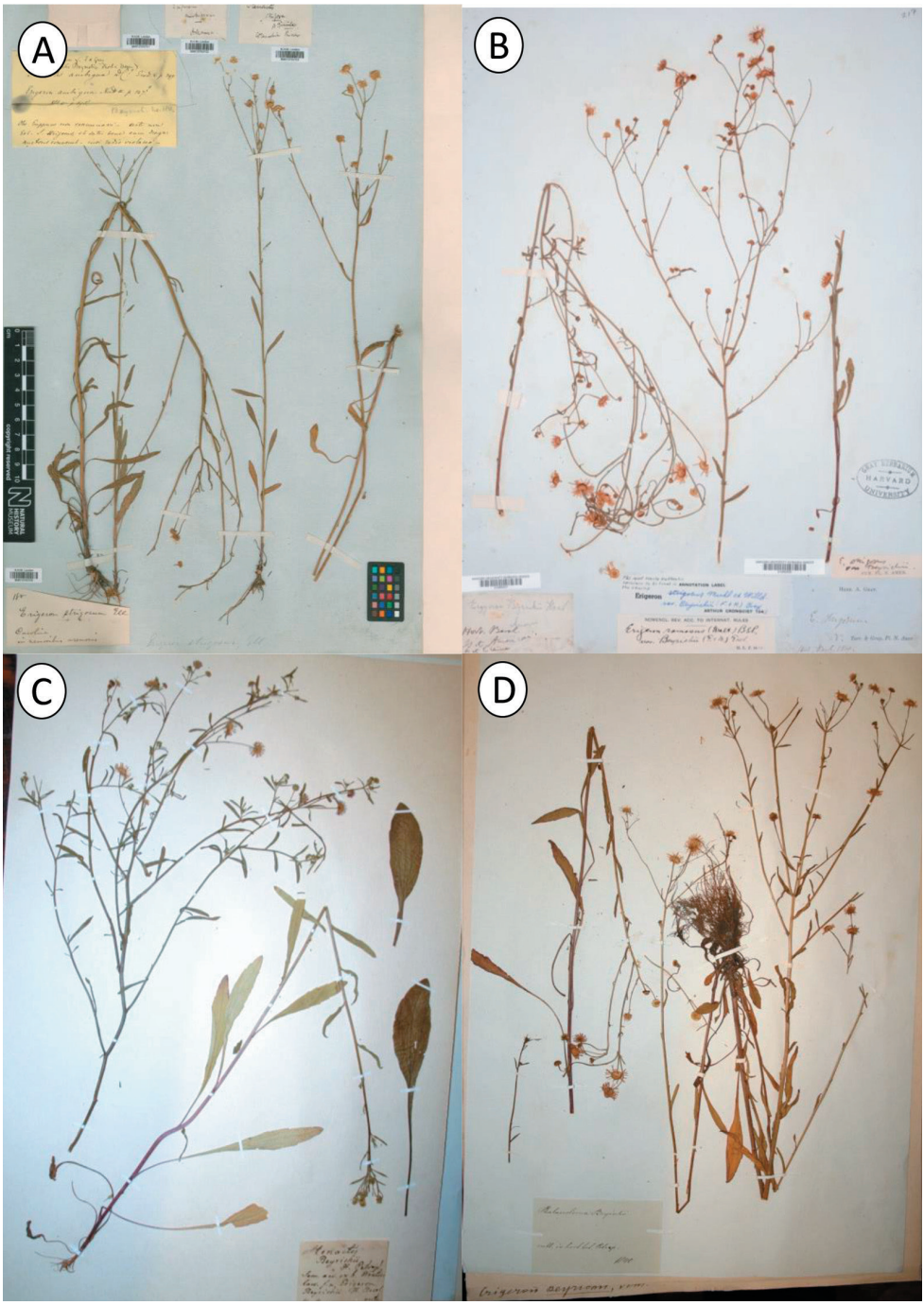

Fig 3. Relevant historical herbarium specimens. **A.** *Beyrich 180* (BM), presumed duplicate of the GA specimen, showing Shuttleworth's annotation (yellow, upper left). **B.** HUH specimen collected by A. Gray at Berlin (B) in 1839 from garden plants grown from seed from specimens sent by Beyrich. **C.** Presumed holotype of *Stenactis beyrichii* (published 1839) at LE, with note by C.A. Meyer indicating that it was grown from seed acquired from Wratislaw (Wroclaw). **D.** Additional specimen at LE bearing the combination *Phalacroloma beyrichii*, published in 1840. High resolution digital images may be accessed at https://doi.org/10.5281/zenodo.14743001.

Global Plants database, accessed September 2024). The nearly identical labeling on the BM and GA Beyrich specimens and their general morphological similarity supports their duplicate status. GA was established in the 1920s (Moore & Giannasi 1994), but the circumstances by which GA acquired the Beyrich duplicate from BM could not be ascertained. Beyrich specimens are widely distributed (JSTOR Global Plants database, accessed September 2024) so it is possible that additional duplicates of the *Erigeron* specimen exist, although his set at B were presumably destroyed in WWII. As a side note, Beyrich died of malaria in 1834 (Geiser 1956) so the date of 1836 on the BM and GA specimens must be erroneous.

Pollen for the GA Beyrich collection is unambiguously indicative of the sexual, diploid condition (Fig. 2). Comparison of images of the putative type specimens housed at LE with the BM and GA Beyrich duplicates and the HUH specimen collected by Asa Gray shows morphological similarity. We therefore conclude by deduction that the type specimens for "*beyrichii*' at LE are also probably sexual and diploid. While it is possible that the original collections by Beyrich included both sexual diploid and apomictic polyploid plants, this is considered to be unlikely.

To the best of our knowledge, *Stenactis beyrichii* Fisch. & C.A. Mey. is the oldest name associated with the coastal plain sexual diploid populations. To distinguish them from their apomictic polyploid relatives, we choose to recognize *Erigeron beyrichii* (comb. nov.) to therefore represent sexual diploid populations of "*Erigeron strigosus*" in the Southeastern United States. For the holotype of the new taxon, we designate the specimen at LE annotated as "*Stenactis beyrichii*," with precedence over the LE specimen annotated as "*Phalacroloma beyrichii*," which is a later combination by one year. While apomictic polyploid *E. strigosus* and sexual diploid *E. beyrichii* overlap geographically in the Southeast, the more limited range of the latter, plus its smaller capitula, more extensive inflorescence branching, and diploid pollen type can be used to distinguish the two taxa. Recognition of the sexual diploid coastal plain populations as a distinct taxon will facilitate future work exploring evolution and diversity in the complex. We further note that the present circumscription that restricts *E. beyrichii* to the southeastern United States excludes plants that occur further north and west previously included as that taxon by Cronquist (1947). We consider it likely that those geographic outliers are apomictic variants of *E. strigosus*. For instance, a roadside plant from Indiana (STIN06; Noyes & Givens 2013), identified as *E. strigosus var. beyrichii* based on morphology, was determined to be triploid and apomictic and therefore better classified with other apomicts as *E. strigosus*.

New Combination

Erigeron beyrichii (Fisch. & C.A. Mey.) Noyes & D.B. Poind., **comb. et stat. nov.** Basionym: *Stenactis beyrichii* Fisch. & C.A. Mey., Index Seminum [St. Petersburg] 5:#2169. 1839. Type: *Stenactis beyrichii*, "Sem acc. ex h. Wratislaw" (holotype: LE). (Fig. 3C).

Phalacroloma beyrichii (Fisch. & C.A. Mey.) Fisch. & C.A. Mey., Index Seminum [St. Petersburg] 6:63. 1840. *Erigeron strigosus* Muhl. ex Wild. var. *beyrichii* (Fisch. & C.A. Mey.) A. Gray, Syn. Fl. N. Amer. 1(2):219. 1884. *Erigeron ramosus* Raf. var. *beyrichii* (Fisch. & C.A. Mey.) Trelease, Rep. Ark. Geol. Surv. 1888(4):192. 1891.

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REFERENCES

Bayer, R. 1987. Evolution and phylogenetic relationships of the *Antennaria* (Asteraceae: Inuleae) polyploid agamic complexes. Biol. Zent. Bl. 106:683–698.

Bierzychudek, P. 2012. The demographic consequences of sexuality and apomixis in *Antennaria*. Biol. Approaches Evol. Trends Pl. 2012:293.

Brendel, F. 1879. Historical sketch of the science of botany in North America from 1635 to 1840. Amer. Nat. 13:754–771.

British Museum (Natural History). 1906. The history of the collections contained in the Natural History Departments of the British Museum, London, UK. Order of the Trustees. (Vol. 2).

Burgess, M.B., K.R. Cushman, E.T. Doucette, N. Talent, C.T. Frye, & C.S. Campbell. 2014. Effects of apomixis and polyploidy on diversification and geographic distribution in *Amelanchier* (Rosaceae). Amer. J. Bot. 101:1375–1387.

Cronquist, A. 1947. Revision of the North American species of *Erigeron*, north of Mexico. Brittonia 6:121–302.

Fischer, F.E.L. & C.A. Meyer. 1840. Index Seminum (St. Petersburg) 6:63.

Geiser, S.W. 1956. Heinrich Carl Beyrich in Arkansas Territory, 1834. Field & Lab. 24:77–96.

Grant, V. 1981. Plant speciation, ed. 2. Columbia Univ. Press, New York, U.S.A.

Hörandl, E. 2014. Nothing in taxonomy makes sense except in the light of evolution: examples from the classification of *Ranunculus*. Ann. Missouri Bot. Gard. 2014:14–31.

Moore, M.O. & D.E. Giannasi. 1994. Vascular plant type specimens in the University of Georgia Herbarium, with a brief history of the herbarium. Sida 16:139–151.

Nesom, G.L. 1989. Infrageneric taxonomy of New World *Erigeron* (Compositae: Astereae). Phytologia 67:67–93.

Nesom, G.L. 2006. *Erigeron*. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 25+ vols. New York, U.S.A. and Oxford, UK. 20:256-348.

Noyes, R.D. 2007. Reticulation and the evolution of apomixis in *Erigeron* sect. *Phalacroloma* (Asteraceae). In: Hörandl, E., U. Grossniklaus, P. Van Dijk, T. Sharbel, eds. Apomixis: evolution, mechanisms and perspectives. Regnum Veg. 147:337–358.

Noyes, R.D. & J.R. Allison. 2005. Cytology, ovule development and pollen quality in sexual *Erigeron strigosus* (Asteraceae). Int. J. Pl. Sci. 166:49–59.

Noyes, R.D. & A.D. Givens. 2013. Quantitative assessment of megasporogenesis for the facultative apomicts *Erigeron annuus* and *Erigeron strigosus* (Asteraceae). Int. J. Pl. Sci. 174:1239-1250.

Stanley, R.G. & H.F. Linskens. 1974. Viability tests. In: Pollen: biology, biochemistry, and management. Springer, Berlin, Germany. Pp. 67–86.

Stebbins, G.L. 1950. Variation and evolution in plants. Columbia Univ. Press, New York, U.S.A.

Weakley, A.S. (& 14 others). 2017. New combinations, rank changes, and nomenclatural and taxonomic comments in the vascular flora of the southeastern United States. II. J. Bot. Res. Inst. Texas 11:291–325.

Weakley, A.S. (& 11 others). 2018. New combinations, rank changes, and nomenclatural and taxonomic comments in the vascular flora of the southeastern United States. III. J. Bot. Res. Inst. Texas 12:27–67.