HELIANTHUS WACCAMAWENSIS (ASTERACEAE), A NEW SPECIES OF SUNFLOWER ENDEMIC TO THE CAPE FEAR ARCH REGION OF NORTH AND SOUTH CAROLINA (U.S.A.)

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ABSTRACT

A new species of *Helianthus* (Asteraceae), **Helianthus waccamawensis** Ungberg, sp. nov., is described from the Cape Fear Arch Region of North and South Carolina. Most recently, it has been included in *H. floridanus* A. Gray ex Chapm. but differs in its narrower leaves, achene and floral morphology, and habitat preferences. It superficially resembles *H. angustifolius* L. but differs in its extensively rhizomatous habit, shorter leaves, and achene and floral morphologies. It is further differentiated from the diploids *H. floridanus* and *H. angustifolius* by being hexaploid, and molecular phylogenetic data do not indicate a close relation to either species. *In situ* photos, diagnostic morphological photos, molecular phylogenetic data, cytological data, a range map, a list of additional collections, and a revised key for relevant southeastern *Helianthus* species are provided.

RESUMEN

Una nueva especie de *Helianthus* (Asteraceae), **Helianthus waccamawensis** Ungberg, sp. nov., es descrita de la región del Cape Fear Arch en Carolina del Norte y del Sur. Recientemente, ha sido incluida en *H. floridanus* A. Gray ex Chapm., pero se diferencia por sus hojas más estrechas, la morfología de los aquenios y flores, y sus preferencias de hábitat. Superficialmente se asemeja a *H. angustifolius* L., pero se distingue por su hábito rizomatoso extenso, hojas más cortas, y la morfología de los aquenios y flores. Además, se diferencia de los diploides *H. floridanus* y *H. angustifolius* por ser hexaploide, y los datos filogenéticos moleculares no indican una relación cercana con ninguna de las dos especies. Se proporcionan fotos in situ, fotos morfológicas diagnósticas, datos filogenéticos moleculares, datos citológicos, un mapa de distribución, una lista de colecciones adicionales y una clave revisada para las especies relevantes de *Helianthus* del sureste.

Key Words: *Helianthus*, Cape Fear Arch, phylogeny, cytology, polyploidy, biogeography, morphometric analysis

INTRODUCTION

The treatment of the genus *Helianthus* L. in Flora of North America (Schilling 2006) recognizes 52 species and one hybrid. While this work represents a significant benchmark in our taxonomic understanding of *Helianthus*, the subsequent discovery of three new species within the genus (Stebbins et al. 2013; Keil & Elvin 2014; Draper & Esque 2021) highlights the need for further taxonomic investigation within this famously

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biologically complex group. In the Southeastern United States, *Helianthus* species are found in a diversity of ecological niches and range from widespread generalists, such as the perennial *H. angustifolius* L., to narrowly endemic edaphic specialists, such as the annual *H. porteri* (A. Gray) Pruski. One such narrowly endemic *Helianthus* entity has historically been confused with several species since its initial collection in 1927, most recently *H. floridanus* A. Gray ex Chapm. This entity is restricted to the Cape Fear Arch (CFA) region of southeastern North Carolina and northeastern South Carolina, an area renowned for its numerous endemic plant species (LeBlond 2001; Sorrie & Weakley 2001), including the iconic Venus Flytrap (*Dionaea muscipula* Ellis). In this study, we investigate this unusual *Helianthus* entity, determining it to be a new species and naming it *H. waccamawensis* Ungberg in honor of the Waccamaw Siouan Tribe and their ancestral lands.

The unusual CFA *Helianthus* entity, herein named *H. waccamawensis* and previously thought to represent the northernmost populations of *H. floridanus* (Figs. 1 and 2), has posed taxonomic challenges due to its atypical morphology. Since the discovery of these populations, botanists have differed in their assessments of their identity. In *The North American Sunflowers* (Heiser et al. 1969), specimens of *H. waccamawensis* examined by Heiser were attributed to *H. schweinitzii*. These specimens represented the disjunct coastal plain records depicted on his range maps for that species. *Helianthus schweinitzii* is a rare species of prairie remnants and pine-oak savannas over rocky and clayey soils in the Piedmont region, making its presence in very dissimilar habitats in the Coastal Plain implausible. Following the federal listing of *H. schweinitzii* as endangered in 1990, further investigations into its range, life history, and habitat were conducted, leading to redetermining these CFA populations initially as *H. angustifolius* (U.S. Fish and Wildlife Service 1994) and then as *H. floridanus* (Matthews et al. 1997). However, the CFA plants differed from typical *H. floridanus* populations found further south in lacking the characteristic undulate leaf margins, exhibiting narrower, more linear leaves, possessing more slender, wiry stems, and occurring in drier habitats (Fig. 1).

The atypical morphology of the CFA populations of "*Helianthus floridanus*" was informally hypothesized to result from introgression with the closely related *H. angustifolius* (Legrand et al. 2021). Fertile hybrids of *H. floridanus* and *H. angustifolius* have been produced experimentally and observed in natural settings (Heiser et al. 1962). In Georgia and Florida, morphologically "typical" individuals of both species occur in close proximity and appear to intergrade morphologically (Heiser et al. 1969; E. Ungberg, pers. obs.). On this basis, Heiser et al. (1969) questioned whether it might be preferable to recognize a broadly conceived taxon that encompassed both *H. floridanus* and *H. angustifolius*. Subsequent phylogenetic analyses have provided further evidence that the two species are closely related, forming a clade with a third species, *H. simulans* E. Watson (Schilling et al. 1998; Timme et al. 2007; Stephens et al. 2015). *Helianthus waccamawensis* might initially seem best placed within this lineage, since it superficially appears to be an intermediate between *H. floridanus* and *H. angustifolius*. However, the naturally occurring intermediates are morphologically distinctive compared to *H. waccamawensis* (E. Ungberg, pers. obs.). Furthermore, true *H. floridanus* does not occur within the range of *H. waccamawensis* (Fig. 2) and, therefore, is unlikely to be a potential parent of any hybrid *Helianthus* entity in the CFA region. *Helianthus waccamawensis* is readily distinguished from both *H. floridanus* and *H. angustifolius* morphologically, and our molecular phylogenetic and cytological evidence does not indicate a close relationship to either species.

Helianthus waccamawensis is found within the CFA region in mesic longleaf pine savannas and roadside habitats with similar hydrological and disturbance characteristics. The CFA region, shaped by intermittent tectonic uplift beginning in the late Cretaceous (Gohn 1988), extends approximately from Cape Lookout, North Carolina to Cape Romain, South Carolina, and reaches inland to Fayetteville, North Carolina. In this region, uplifted Cretaceous strata extend nearly to the modern coastline, elevating the terrain relative to adjacent areas of the Albemarle embayment to the north and the Charleston embayment to the south (Walker & Coleman 1987). This regional transformation of landscape topography allowed the upland areas of the CFA to remain unflooded during past interglacial periods that submerged much of the surrounding Atlantic Coastal Plain (Colquhoun et al. 1981). Periodic isolation of this region from lower-elevation areas, coupled with the distinctive soils typically found in the Coastal Plain, likely facilitated the evolution of the unique flora of the

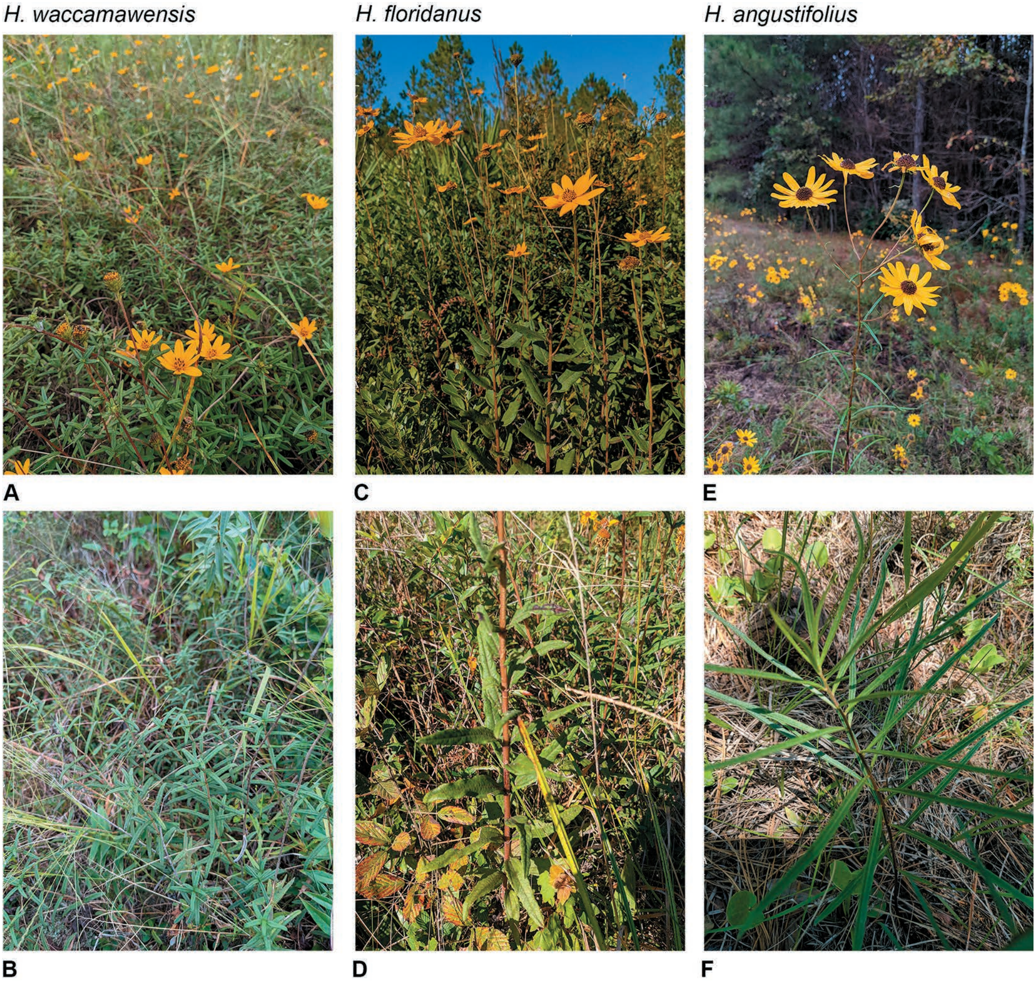


Fig. 1. Comparison of leaves and habit of *Helianthus waccamawensis* and morphologically similar species. *Helianthus waccamawensis* roadside population, Horry Co., SC (A). *Helianthus waccamawensis* rhizomatous habit, with small, opposite decussate, gray-green leaves, Columbus Co., NC (B). *Helianthus floridanus* rhizomatous habit and gestalt in boggy roadside swale, Clay Co., FL (C). *Helianthus floridanus* typical lanceolate leaf shape with undulate margins and robust stems, McIntosh Co., GA (D). *Helianthus angustifolius* roadside population showing typical stature, and inflorescences with many capitula, Lee Co., NC (E). *Helianthus angustifolius* narrowly linear, bright green leaves, Brunswick Co., NC (F).

CFA region (LeBlond 2001; Sorrie & Weakley 2001). The CFA remains fertile ground for the discovery of new endemic plant species, including the recently described *Rhynchospora croatanensis* LeBlond & P.D. McMillan (McMillan & LeBlond 2024), *Dichanthelium freckmannii* LeBlond (LeBlond et al. 2024), *Coreopsis aristulata* LeBlond, Sorrie, & Weakley (Sorrie et al. 2013), and several more that are hypothesized but not yet named (e.g., *Hypericum* sp. 2, *Allium* sp. 1; Weakley & Southeastern Flora Team 2024).

In this study, we investigate the taxonomic biology of *H. waccamawensis* using new evidence from comparative morphometrics, cytology, and molecular phylogenetics. We discuss these data in the context of all available information to establish its distinctiveness and propose a hypothesis regarding its allopolyploid origin. Further, we explore the phytogeography, ecology, and conservation status of this globally imperiled new species.

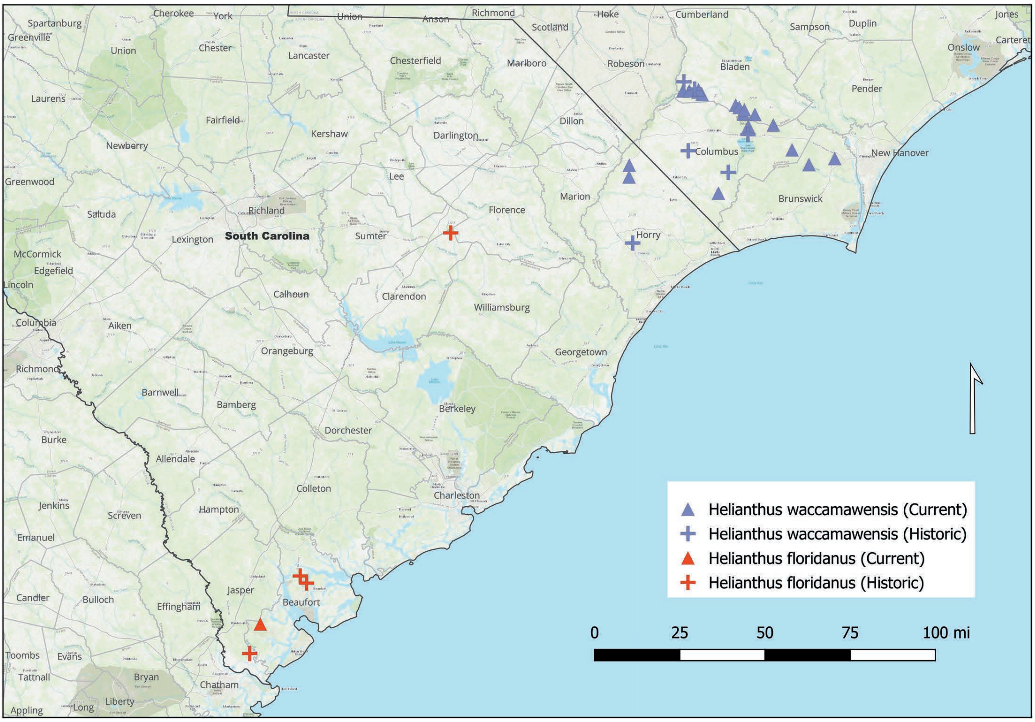


Fig. 2. Range map showing all known current (Δ) and historic (+) populations of *H. waccamawensis* (blue) and *H. floridanus* (red) in North and South Carolina. Map created using open source QGIS software version 3.16.9-Hannover.

METHODS

Morphometric Comparison.—Potential locations of *Helianthus angustifolius*, *H. floridanus*, and *H. waccamawensis* were gathered from several sources, including Natural Heritage Program data layers from North and South Carolina, herbarium specimens (mostly via the Southeast Regional Network of Expertise and Collections; SERNEC 2024), iNaturalist (2024) observations, and through personal communication with other field botanists working in the area, principally Keith Bradley of the South Carolina Department of Natural Resources and Alicia Jackson of J.H. Carter III and Associates. Specimens collected during Fall 2021 fieldwork were combined with existing collections at North Carolina State University (NCSU), Duke University (DUKE), and University of North Carolina at Chapel Hill (NCU) for the collection of morphometric data.

Species selected for the comparative morphometric analysis were based on previous identifications, species ranges, and our impression of general similarity. Specimens of *H. waccamawensis* have been attributed to four different taxa and one infraspecific taxon – *H. angustifolius* L., *H. angustifolius* L. var. *planifolius* Fernald, *H. floridanus* A. Gray ex Chapm., *H. heterophyllus* Nutt., and *H. schweinitzii* Torr. & A. Gray. We limited the species for comparison to just *H. angustifolius* and *H. floridanus*. We included *H. angustifolius* because it is superficially the most similar in overall gestalt and appearance and occurs sympatrically with *H. waccamawensis*. We included *H. floridanus* because it is the species most recently and widely confused with *H. waccamawensis*. *Helianthus heterophyllus* was excluded from this analysis because it differs obviously from the aforementioned species in its cespitose habit and basally disposed leaves. *Helianthus schweinitzii* was also excluded because it is a much larger plant with numerous distinguishing characteristics, including tuberous rhizomes, and it occurs exclusively in the Piedmont region of the Carolinas.

We collected measurement data for 12 continuously variable and one meristic character (13 characters total; Table 1) from herbarium specimens of the three above-mentioned species. Characters commonly used to distinguish species in *Helianthus* were prioritized (e.g., leaf vestiture, leaf length, leaf width, plant height and size, achene shape and size, pappus scale shape and size, etc.; Radford et al. 1968; Heiser et al. 1969; Schilling 2006; Weakley & Southeastern Flora Team 2024). Specimens used in the morphological analysis met two criteria: (1) they consisted of reproductive plants in early flower or later stages, and (2) they included the entire above-ground portion of the plant. Measurements taken in millimeters were made with a 0.1 mm micrometer. Measurements taken in centimeters were made with a standard metric ruler. Specimens with more than one stem had an equal number of replicate measurements made (one per stem) for maximum leaf length, maximum leaf width, number of capitula, basal stem width, and stem height. For leaf dimensions, the longest and widest leaves from the middle 50% of each stem were chosen for those respective measurements. For abaxial trichome length, a mid-stem leaf was selected at random and five trichomes were measured, selecting the largest and most prominent. Achenes and/or disc florets were extracted at random from mature capitula on each specimen. Achenes (and pappus scales) and disc florets did not always come from the same capitula, as some capitula with mature achenes had disc florets that had mostly begun to senesce, and some capitula with disc florets in good condition lacked mature achenes. Achene pappus scale measurements were generally taken from random, but otherwise whole and undamaged, pappus scales produced during achene/disc floret extraction, due to their tendency to disarticulate from the achene. For all achene, pappus scale, and disc floret characters, three measurements were made per specimen.

Using JMP® v16 (2022–2023), we performed multiple, pairwise comparisons of the least squared means for each of the 13 characters using the Student's t-test to assess significant differences between these means across the three species studied. We did not apply a *post hoc* correction to adjust for multiplicity due to the limited number of planned comparisons, which reduces the risk of an inflated Type I error rate (Rothman 1990; Midway et al. 2020). The significant figures for the raw means reported in Table 1 reflect the precision of the measurements taken.

Cytology.—Meiotic chromosomes were examined following standard procedures (Beeks 1955) using early flowering material collected *in situ* in September and October 2021 from several roadside populations in Bladen Co. (NCU00448051, NCU00448055) and Columbus Co. (NCU00448059, NCU00448050), NC, and from a population in Horry Co., SC, in August 2024 (*Ungberg s.n.*, specimen not yet processed). Young capitula were fixed for at least 24 hours in Carnoy I solution, and unused material was transferred to 70% ethanol for storage. Counts were made from a minimum of 5 cells displaying adequately spaced meiotic figures from two or more individuals within each of the three aforementioned populations. Visualization was attained by squashing anthers in acetocarmine stain, followed by clearing and stabilization with Hoyer's Mounting Medium. Images of cells in late diakinesis through early metaphase II at 1000× magnification were taken using a Leica DMLS phase contrast trinocular microscope with a Canon Mark II DSLR camera attachment.

Molecular Phylogenetics and Evolution.—Leaf tissue samples were preserved in silica gel for subsequent DNA extraction during Fall 2021 fieldwork by Author 1 (see Table 2). Total genomic DNA was extracted from each sample using the DNeasy Plant Mini Kit (QIAGEN, Valencia, CA). PCR amplification of the nuclear ribosomal (nr) External Transcribed Spacer (ETS) region followed the protocol and primers described by Timme et al. (2007). Since this new *Helianthus* entity was determined to be a hexaploid, molecular cloning was employed to isolate ETS amplicons using the TOPO TA Cloning^{TM} Kit for Sequencing (Invitrogen, Waltham, MA). Successful transformants were obtained exclusively using DH5-α High Efficiency *E. coli* competent cells (New England Biolabs, Ipswich, MA). Fifteen colony PCR products were sent to Eurofins Genomics (Louisville, KY) for automated Sanger sequencing using all six primers described by Timme et al. (2007). Chromatogram reads were edited using Sequencher (Gene Codes, Ann Arbor, MI). We recovered sequences of five different ETS amplicon types for *H. waccamawensis*, derived from two individuals from separate populations (Table 2). The sequences vary in length: isolate 2 is 1578 bp in length (unaligned), whereas the other four isolate types range from 2098 bp to 2122 bp.

Table 1. Comparison of mean values (± standard error of mean) of measurements of 13 vegetative and reproductive characters for *Helianthus waccamawensis, H. angustifolius, and H. floridanus*. The significance of the differences between the mean values of the three taxa for each character was determined by conducting a Student's t-test for all pairwise comparisons among the four taxa. Taxa not sharing the same letter have significantly different mean values for a given character at α = 0.05. Shading indicates that the mean value of a given character for *H. waccamawensis* is significantly different (α = 0.05) from all three other taxa examined.

Character	H. angustifolius (n=17)	H. floridanus (n=32)	H. waccamawensis (n=24)
Achene length (mm)	2.9 (± 0.10) a	3.2 (± 0.07) b	3.9 (± 0.06) c
Pappus scale width (mm)	0.2 (± 0.04) a	0.2 (± 0.03) a	0.8 (± 0.03) b
Pappus scale length (mm)	1.8 (± 0.12) a	2.3 (± 0.0.08) b	2.0 (± 0.08) ab
Disc floret diameter (mm)	1.5 (± 0.09) a	1.8 (± 0.05) b	2.8 (± 0.07) c
Disc floret lobe length (mm)	0.5 (± 0.05) a	0.7 (± 0.03) b	1.3 (± 0.04) c
Disc floret length (mm)	3.4 (± 0.09) a	3.9 (± 0.06) b	5.4 (± 0.08) c
Disc floret tube width (mm)	0.7 (± 0.03) a	0.9 (± 0.02) b	1.2 (± 0.03) c
Maximum leaf length (cm)	14.1 (± 0.41) a	7.7 (± 0.35) b	5.0 (± 0.35) c
Maximum leaf width (mm)	4.5 (± 0.81) a	17.2 (± 0.69) b	4.0 (± 0.68) a
Abaxial trichome length (mm)	0.6 (± 0.03) a	0.3 (± 0.03) b	0.8 (± 0.03) c
Number of heads (n)	10.2 (± 0.87) a	3.8 (± 0.75) b	2.5 (± 0.74) b
Basal stem width (mm)	4.6 (± 0.21) a	4.0 (± 0.16) b	1.9 (± 0.16) c
Stem height (cm)	102 (± 4.7) a	95 (± 4.0) a	53 (± 4.0) b

Table 2. Voucher information and GenBank accession numbers for sequences of *Helianthus* ETS amplicon isolates newly generated for this study. GenBank accession numbers for ETS sequences generated or used by Timme et al. (2007) are given in Fig. 6.

Taxon	Isolate number, given in Fig. 6	Voucher	Source	GenBank accession No.
H. waccamawensis	2	Ungberg 827 (NCU)	Columbus Co., NC, U.S.A.	PQ469699
H. waccamawensis	3	Ungberg 827 (NCU)	Columbus Co., NC, U.S.A.	PQ469700
H. waccamawensis	6	Ungberg 827 (NCU)	Columbus Co., NC, U.S.A.	PQ469701
H. waccamawensis	11	Ungberg 769 (NCU)	Bladen Co., NC, U.S.A.	PQ469697
H. waccamawensis	13	Ungberg 769 (NCU)	Bladen Co., NC, U.S.A.	PQ469698
H. angustifolius	Not applicable	Ungberg 765 (NCU)	Bladen Co., NC, U.S.A.	PQ469696

To assess the phylogenetic placement of the *Helianthus waccamawensis* ETS isolate sequences, we retrieved *Helianthus* ETS isolate sequences from GenBank (Clark et al. 2016) that Timme et al. (2007) used in their comprehensive genus-wide phylogenetic study. GenBank accession numbers for these sequences are given in Fig. 6. We opted to use ETS because the phylogenetic framework provided by Timme et al. (2007) offers better topological resolution, branch support, and sampling compared to phylogenies based on nr ITS sequences (Schilling et al. 1998) or chloroplast restriction sites (Schilling 1997). Furthermore, Timme et al. (2007) thoroughly examined their ETS amplification products from each accession using molecular cloning to explore for and recover polymorphic copies resulting from hybridization (homeologs) and variation among tandem repeats.

We sampled 42 sequences from 24 non-hybrid diploid *Helianthus* species included in Timme et al. (2007), representing all major clades resolved in their analysis of non-hybrid diploid species, along with 11 sequences from five polyploid species belonging to section *Divaricati* series *Corona-solis* (Schilling & Heiser 1981) that form a clade in their fully sampled analysis. We excluded several non-hybrid diploid species from Clade 3 of the analysis of non-hybrid diploids in Timme et al. (2007) because preliminary analyses indicated that they did not contribute to understanding the phylogenetic placement of the *H. waccamawensis* ETS isolate sequences. Our inclusion of all sequences from the polyploid clade just mentioned was also based on preliminary analyses that suggested a relationship between our *H. waccamawensis* ETS isolates and those of *H. schweinitzii*.

We conducted the multiple sequence alignment using MUSCLE v5 (Edgar 2022), then adjusted the resulting alignment by eye to ensure the comparison of orthologous subrepeats, as described by Timme et al. (2007). We determined the best-fit model of sequence evolution for the ETS dataset using PAUP* v4.0a Build 169 (Swofford 2002). The analysis selected the TVM+Γ model using the Bayesian Information Criterion (Schwarz 1978), and we set the starting model and prior parameters of subsequent phylogenetic analyses to be consistent with these results. We conducted all phylogenetic analyses using the CIPRES Science Gateway (Miller et al. 2010). Maximum Likelihood phylogenetic analyses, including bootstrap analyses (1000 pseudo-replicates) to assess branch support, were conducted with RAxML v8.2.12 (Stamatakis 2014). Bayesian phylogenetic analyses were performed using MrBayes v3.2.7a (Ronquist et al. 2012) using four concurrent runs of 4×10^7 generations, with each run consisting of one cold chain and three incrementally heated chains. The temperature parameter was set to 0.2, and the cold chain was sampled every 1000 generations. Convergence diagnostics were evaluated with Tracer v1.7.2 (Rambaut et al. 2018). We used a burn-in of 1×10^7 generations (25% of the generations in each run), which was substantially more conservative than indicated by the log likelihood plot in Tracer v1.7.2. Trees from the post burn-in period of the four runs (1.2×10^5 trees in total) were pooled to determine the Bayesian posterior probability values.

Given the known challenges of using nr DNA to infer the phylogenetic placement of hybrids and allopolyploids (Soltis et al. 2008), we interpreted our phylogenetic results as representing a gene tree that differs from subsequent estimations of the true species tree (e.g., Stephens et al. 2015, for diploids only). We primarily used it to rule out some of our initial hypotheses of the ancestral parentage of *H. waccamawensis* and also to provide supporting evidence for a broad hypothesis of the relationship of one putative parent.

RESULTS

Morphometric Comparison.—Table 1 summarizes the results of the multiple, pairwise comparisons using the Student's t-test across the three species and 13 morphometric traits we investigated. Figure 1 shows general differences in gestalt and growth habit among the three species examined. *Helianthus waccamawensis* has significantly narrower ($\bar{x} = 4.0$ mm vs. 17 mm; $p < 0.001$) and shorter ($\bar{x} = 5.0$ cm vs. 7.7 cm; $p < 0.0001$) leaves compared to *H. floridanus*. Although similar in width to *H. angustifolius* (Fig. 3), the leaves of *H. waccamawensis* are significantly shorter ($\bar{x} = 5.0$ cm vs. 14.1 cm; $p < 0.0001$). Abaxial leaf vestiture also varies, with *H. waccamawensis* having longer trichomes ($\bar{x} = 0.8$ mm) than both *H. angustifolius* ($\bar{x} = 0.6$ mm; $p < 0.001$) and *H. floridanus* ($\bar{x} = 0.3$ mm; $p < 0.0001$; Fig. 3).

Among the three species, *H. waccamawensis* has the largest disc florets across several trait dimensions, including corolla width, the length of the largest corolla lobe, and the width and length of the largest corolla tube ($p < 0.0001$ for all comparisons). *H. waccamawensis* produces fewer capitula per stem ($\bar{x} = 2.5$) compared to *H. floridanus* ($\bar{x} = 3.8$; not significant) and *H. angustifolius* ($\bar{x} = 10.2$; $p < 0.0001$). The mean achene length in *H. waccamawensis* is significantly longer than that of both *H. floridanus* and *H. angustifolius* ($p < 0.0001$ for both comparisons; Fig. 4). Additionally, *H. waccamawensis* has pappus scales that are nearly three times wider than those of the other two species ($p < 0.0001$ for both comparisons; Fig. 4).

In terms of overall structure, *H. waccamawensis* is a more delicate plant, with finer stems ($\bar{x} = 1.9$ mm, for basal stem diameter) than both *H. angustifolius* and *H. floridanus*, whose stem bases average 4.0 mm or greater in diameter ($p < 0.0001$ for both comparisons). Finally, *H. waccamawensis* is shorter in stature, with a mean height of 53 cm, compared to 95 cm or greater for the other two species ($p < 0.0001$ for both comparisons).

The measurements from our morphometric study are largely consistent with those provided for *H. angustifolius* and *H. floridanus* in the Flora of North America (Schilling 2006), with one noted discrepancy. We found that the disc florets of *H. angustifolius* were generally shorter than reported, averaging 3.4 mm compared to the published range of 4.0–4.5 mm. Although the value of the mean disk floret length in *H. angustifolius* may increase with a larger sample size, in areas where it is sympatric with *H. waccamawensis*, *H. angustifolius* consistently has smaller disc florets.

Cytology.—Based on chromosome counts carried out on floral material from Bladen and Columbus Cos., NC, and Horry Co., SC, *H. waccamawensis* is hexaploid (Fig. 5; $n=51$, base number of $x=17$). Although

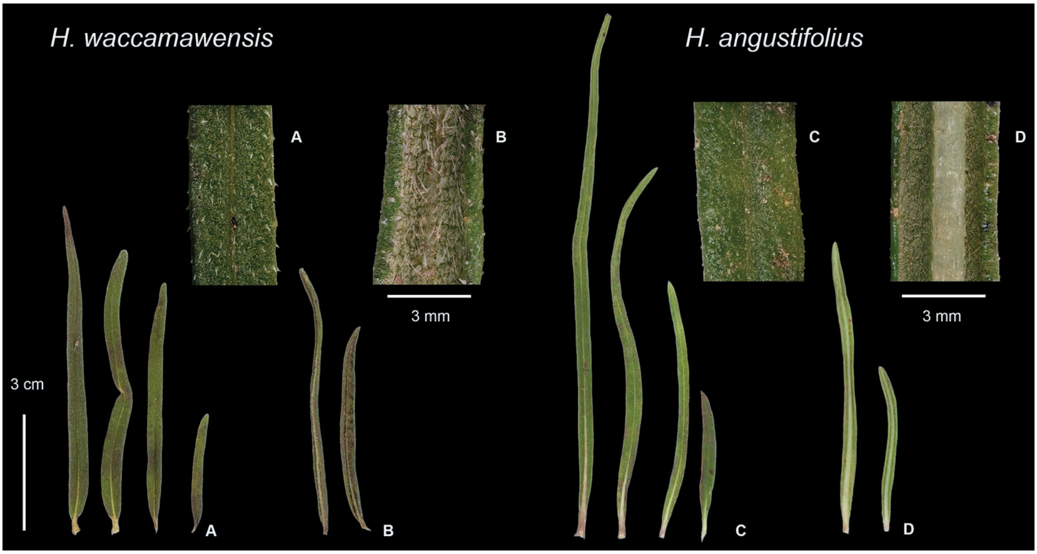


Fig. 3. Comparison of general leaf morphology of *H. waccamawensis* and *H. angustifolius*. *Helianthus waccamawensis* adaxial leaf gestalt and surface detail (**A**). *Helianthus waccamawensis* abaxial leaf gestalt and surface detail (**B**). *Helianthus angustifolius* adaxial leaf gestalt and surface detail (**C**). *Helianthus angustifolius* abaxial leaf gestalt and surface detail (D).

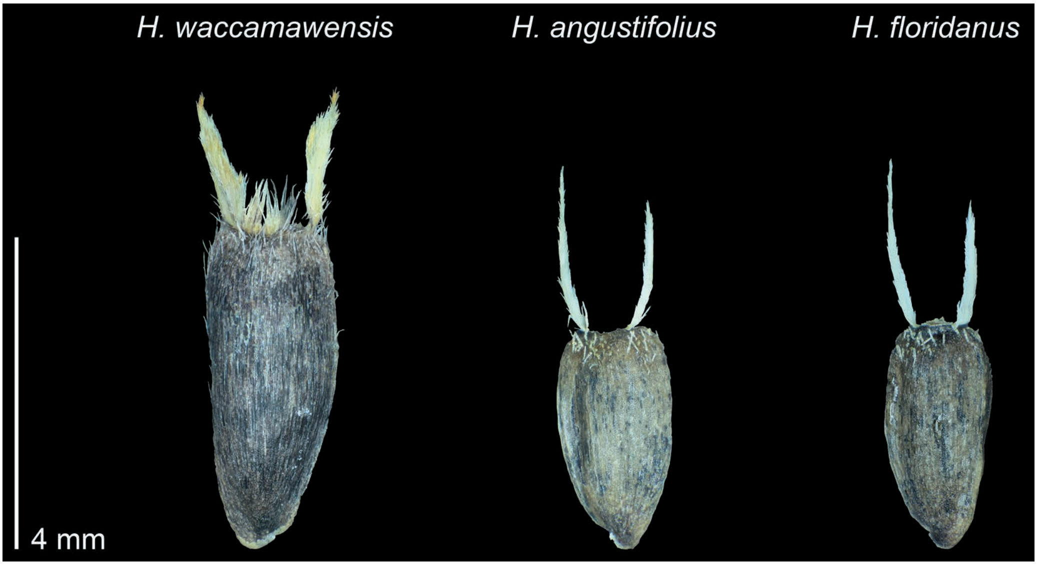


Fig. 4. Detail of *H. waccamawensis* disc floret and achene (**left**), and comparison with *H. floridanus* and *H. angustifolius* achenes (**right**). Achenes B and C are slightly smaller than average for their respective species.

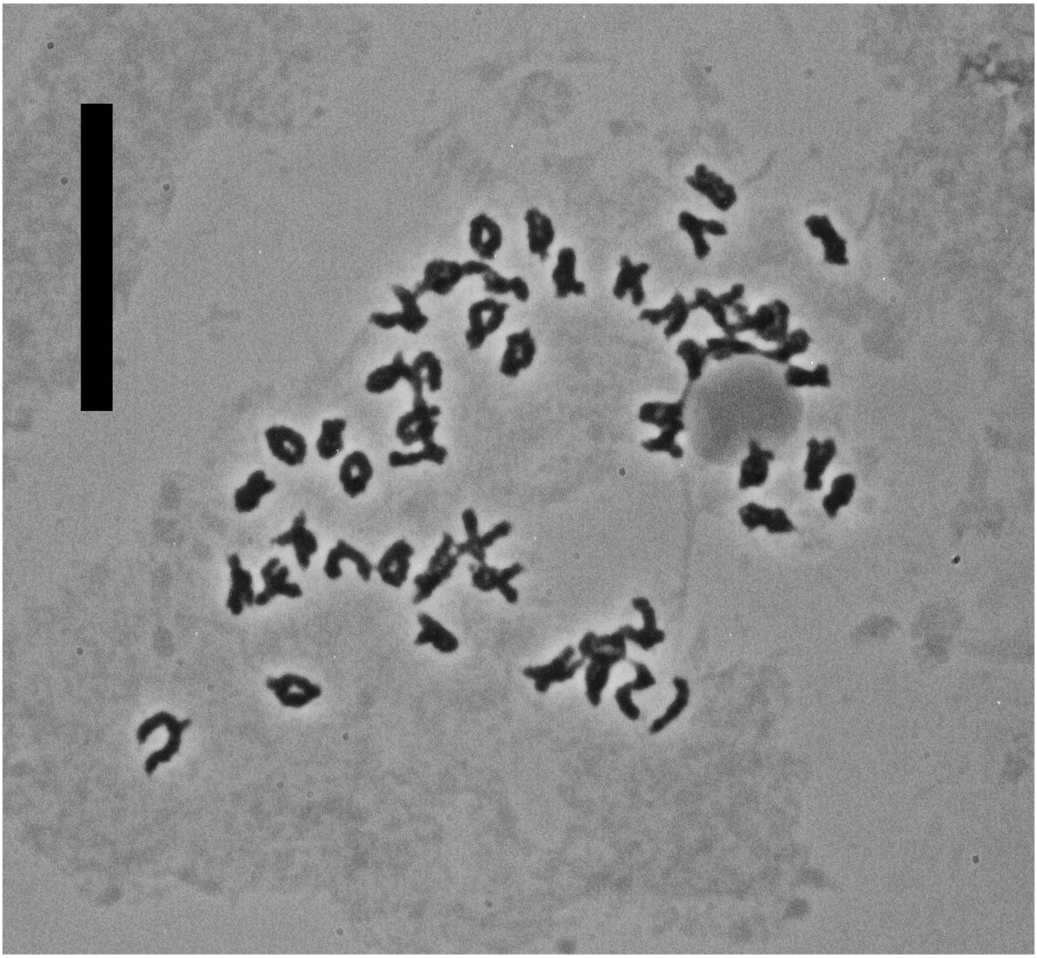


Fig. 5. Meiotic chromosome photomicrograph of *Helianthus waccamawensis* (n = 51; voucher: *E.A. Ungberg 764*, Bladen Co., NC, Holotype: NCU). Scale bar = 10 µm.

several populations were collected in 2021, only one usable count (from Bladen Co., NCU00448051) was ultimately obtained, leading us to obtain a second count with material collected from Horry Co., SC, in August of 2024.

Molecular Phylogenetics and Evolution.—The final aligned matrix of the ETS sequence data was 2684 bp in length. Sequences from the five different ETS amplicon isolates of *H. waccamawensis* (a hexaploid) nest within a moderately- to well-supported clade (BS 83/PP 0.99) of polyploids (Fig. 6) that is congruent with the Group 2 polyploid clade recovered by Timme et al. (2007). This clade also includes isolates from *H. californicus* DC. (hexaploid), *H. eggertii* Small (hexaploid), *H. hirsutus* Raf. (tetraploid), *H. laevigatus* Torr. & A. Gray (tetraploid), and *H. schweinitzii* Torr. & A. Gray (tetraploid; ploidy levels from Timme et al. 2007). Within this polyploid clade, four of the *H. waccamawensis* isolates, together with one isolate of *H. schweinitzii*, form a poorly supported subclade. The fifth *H. waccamawensis* isolate (isolate 2) is nested within a different subclade that also contains two isolates of *H. eggertii*. Within this latter subclade, a sister relationship between *H. waccamawensis* isolate 2 and an *H. eggertii* isolate is moderately to well supported (BS 75/PP 0.99; Fig. 6).

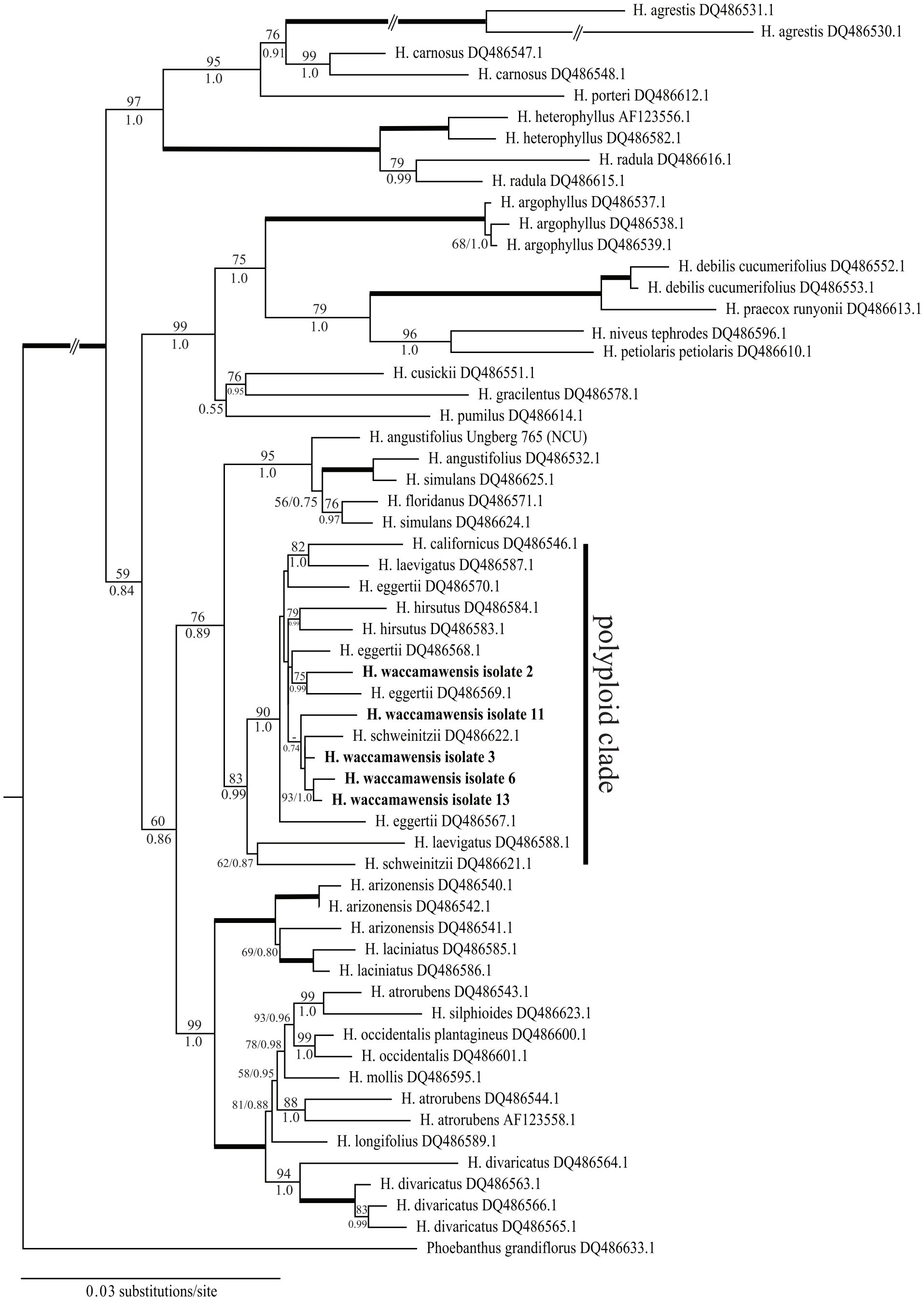


Fig. 6. Phylogeny of *Helianthus* based on ETS sequence data. Tree topology and branch lengths are the optimal Maximum Likelihood (ML) tree. ML bootstrap values are indicated above associated branches; a dash indicates a bootstrap value < 50%. Bayesian posterior probability values are indicated below relevant branches (or to right of slash). Branches in bold have 100% ML bootstrap and 1.0 Bayesian posterior probability values. Branch lengths are proportional to the number of substitutions/site (legend). Isolates of *H. waccamawensis* are shown in boldface type, and the isolate number corresponds with Table 2. The polyploid clade, indicated by the vertical line, is congruent with the Group 2 polyploid clade of Timme et al. (2007). GenBank accession numbers follow accessions used in Timme et al. (2007).

DISCUSSION

A synthesis of the three lines of evidence we provide—morphometric comparison, cytology, and molecular phylogenetics—supports the recognition of *Helianthus waccamawensis* as a distinct species. Our morphometric analysis reveals that 10 of the 13 measured traits significantly distinguish *H. waccamawensis* from both *H. floridanus* and *H. angustifolius* (Table 1), the two species with which it most closely resembles. Two of the three remaining traits significantly distinguish *H. waccamawensis* from one of the remaining species (e.g., leaf width separates *H. waccamawensis* from *H. floridanus* but not *H. angustifolius*). Figures 1, 3, and 4 illustrate the overall morphology of these three species and detail the differences in leaf and achene structure. Additional distinguishing characteristics not included in the morphometric analysis further support the species status of *H. waccamawensis* (E. Ungberg, pers. obs.). For example, the long-rhizomatous growth habit of *H. waccamawensis* reliably differentiates it from *H. angustifolius* in the absence of reproductive material or in populations where the latter species exhibits reduced stature (e.g., roadside populations affected by mowing). The density and length of cilia on the phyllaries of *H. waccamawensis* are also unique among the three species. Furthermore, the phyllaries of *H. waccamawensis* tend to be thicker, particularly at the apex, compared to the other species. The number of pappus scales is another distinguishing feature, as *H. waccamawensis* cypselae frequently have extra, irregularly shaped scales in addition to the two primary pappus scales, a characteristic not observed in either *H. angustifolius* or *H. floridanus*.

Our cytological evidence also supports the recognition of *Helianthus waccamawensis* as a distinct species because it is unique in being hexaploid (Fig. 5) among the species with which it is either confused or co-occurs. Except for the tetraploid *H. schweinitzii* (Matthews et al. 1997), all other species that either co-occur with *H. waccamawensis* (*H. angustifolius*, *H. atrorubens*) or have been confused with it based on morphology (*H. angustifolius*, *H. floridanus*, *H. heterophyllus*) are diploid (Timme et al. 2007).

As a prelude to discussing our ETS phylogeny and its relevance to understanding the evolution of *H. waccamawensis*, we first address some important aspects of the evolution of ribosomal DNA (rDNA) and its significance to the placement of allopolyploid species in rDNA phylogenies. In allopolyploid species, concerted evolution typically leads to the homogenization of rDNA repeats, often toward one of the parental lineages, which erases evidence of ancient hybridization, complicating its detection in rDNA phylogenies (Soltis et al. 2008). In *Helianthus*, the process of rDNA homogenization appears to be incomplete, allowing for the recovery of ETS amplicon isolates of varying lengths, particularly in species presumed to be of allopolyploid origin (Timme et al. 2007). However, despite this incomplete homogenization, concerted evolution in *Helianthus* has been strong enough in most presumed allopolyploid species to effectively obscure the presence of homeologous ETS types, resulting in the predominance of ETS sequences linked to one diploid progenitor (Timme et al. 2007). This pattern is common across rDNA phylogenies of flowering plant lineages that contain allopolyploids (Soltis et al. 2008).

Given the impact of concerted evolution, the placement of *H. waccamawensis* within the polyploid clade (Fig. 6) in our ETS phylogeny should be interpreted as evidence that is principally valuable in refuting certain hypotheses rather than directly supporting a specific hypothesis of origin. All ETS isolate sequences from *H. waccamawensis* nest within the polyploid clade, which was also recovered by Timme & al. (2007; without *H. waccamawensis*). As with ETS isolates from the other species in this clade, the *H. waccamawensis* isolates did not resolve as monophyletic, which is consistent with the process of concerted evolution homogenizing rDNA repeats toward one parental lineage. Concerted evolution, therefore, makes it difficult to trace the exact hybrid origin of *H. waccamawensis* from its ETS sequences alone. Hence, the lack of evidence for homeologous ETS types in *H. waccamawensis* should not be seen as contradictory to a hybrid origin, but as a typical consequence of rDNA molecular evolution in (allo)polyploid species.

With this understanding, we use our molecular phylogenetic evidence to refute the hypothesis that *H. waccamawensis* is an autopolyploid derivative of a member of the clade containing the diploid species *H. angustifolius*, *H. floridanus*, and *H. simulans* (the AFS clade), which is sister to the polyploid clade (Fig. 6). If *H. waccamawensis* were strictly an autopolyploid of one of these species (or their ancestors), its ETS sequences would be expected to nest within or sister to the AFS clade. Instead, the placement of *H. waccamawensis* within the polyploid clade makes this scenario unlikely. This phylogenetic evidence can also refute the hypothesis that *H. waccamawensis* is recently derived allopolyploid with parentage exclusively from AFS clade members, which is broadly consistent with the "introgressed *H. floridanus*" hypothesis of its identity (Legrand et al. 2021). Additionally, *H. waccamawensis* exhibits significant morphological differences from AFS clade members, including smaller leaves, shorter stature, and more slender stems, which are not easily attributable to differences in cytotype alone (Soltis et al. 2007). Furthermore, the sesquiterpene lactone profile of *H. waccamawensis* (Spring & Schilling 1991; see below) does not suggest a close relationship with the AFS clade. These lines of evidence collectively refute the hypothesis that *H. waccamawensis* is an autopolyploid or allopolyploid derived exclusively from AFS clade progenitors.

The hypothesis that *H. waccamawensis* is of allopolyploid origin from perhaps phylogenetically disparate parentage within the genus remains more plausible, especially in the broader context of knowledge of polyploid evolution in *Helianthus*. Heiser & al. (1969) proposed an allopolyploid origin for all species within the polyploid clade (obviously omitting *H. waccamawensis*), invoking diploid species now considered to be phylogenetically distant as parents for most of these polyploids. Recent phylogenomic studies support this general hypothesis. Owens & al. (2023) found widespread evidence of genetic admixture across *Helianthus* species, leading them to suggest that the genus may function as a syngameon, in which reproductively isolated modern species are connected through both ancient and recent gene flow. This syngameon model supports a hypothesis of complex hybrid origins of the perennial polyploid species like *H. waccamawensis* and also supports the idea that *H. waccamawensis* may share an extinct progenitor with other members of the polyploid clade (Timme et al. 2007; Anderson et al. 2019). Alternatively, *H. waccamawensis* may have inherited one of its genomes from an ancestor shared with the AFS clade (Timme et al. 2007). The placement of *H. waccamawensis* within the strongly nested polyploid clade (Fig. 6) supports these inferences (Timme et al. 2007; Soltis et al. 2008), although the contributors to its genome remain unknown.

Phytochemical analyses of *Helianthus* species by Spring and Schilling (1991) may offer additional insights into the ancestry of *H. waccamawensis*. In their extensive survey of sesquiterpene lactones in *Helianthus*, Spring and Schilling (1991) probably conflated *H. schweinitzii* samples with *H. waccamawensis*, as most of their samples of *H. schweinitzii* came from Columbus and Bladen Counties, NC—well outside of the known range of *H. schweinitzii*. These samples were combined with one from Mecklenburg County, NC, which presumably represented true *H. schweinitzii*. Unfortunately, their voucher specimens were kept in personal herbaria and are unavailable for examination, but it is likely that their results for *H. schweinitzii* reflect a mixture of both species, complicating interpretation. Spring and Schilling found that their samples of *H. schweinitzii/H. waccamawensis* shared the largest number of detectable sesquiterpene lactones with *H. heterophyllus*, including several uncommon within the genus. Despite the uncertainty surrounding the sample identities, we believe *H. heterophyllus* (or an ancestor) is a plausible contributor to the genome of *H. waccamawensis*, which is bolstered by the fact that these two species share morphological traits that are rare among *Helianthus* species occurring in the region. Notably, *H. waccamawensis* has supernumerary pappus scales like *H. heterophyllus*, and its principal two pappus scales are much wider than those of *H. angustifolius* and *H. floridanus*.

In conclusion, our synthesis of new morphometric, cytological, and molecular phylogenetic data supports recognizing *Helianthus waccamawensis* as a distinct species. Morphometrically, *H. waccamawensis* shows significant differentiation from *H. floridanus* and *H. angustifolius* in 10 out of 13 measured traits, with additional distinguishing characteristics, such as its long-rhizomatous growth habit and the presence of supernumerary pappus scales, that are not captured in the analysis. Cytologically, *H. waccamawensis* is the only hexaploid among the species with which it co-occurs or is often confused, further supporting its genetic distinctiveness. Molecular phylogenetic evidence based on ETS sequences robustly places *H. waccamawensis* within a clade of polyploid species, suggesting an allopolyploid origin and the possibility it may share an extinct progenitor with other members of the polyploid clade. Although the precise genomic contributors remain unresolved, the phylogenetic, morphometric, and cytological evidence, in combination with a sesquiterpene lactone profile broadly shared with *H. heterophyllus* and geographic isolation in the Cape Fear Arch region, strongly supports the hypothesis that *H. waccamawensis* is a distinct evolutionary lineage of sunflowers. Future research using phylogenomic approaches based on whole genome sequences will be necessary to fully resolve the complex evolutionary history of *H. waccamawensis* and other perennial polyploid *Helianthus* species (Owens et al. 2023).

TAXONOMIC TREATMENT

Helianthus waccamawensis Ungberg, **sp. nov.** (**Figs. 1A, 1B, 3A, 3B, 4A, 7**). Type: U.S.A. North Carolina. Bladen Co.: Bladenboro, W side of Forrest Dr. just N and W of its intersection with Route 410; 34.511670, –78.824863; roadside savanna remnant, with *Lespedeza capitata*, *Helianthus angustifolius*, *Helianthus atrorubens*, *Pteridium pseudocaudatum*, *Clethra alnifolia*, *Rubus* spp., *Smilax* spp., *Muhlenbergia expansa*; 10 Sep 2021, *Ungberg 764* (holotype: NCU).

Diagnosis.—*Helianthus waccamawensis* is morphologically most similar to the sympatric *H. angustifolius*, from which it differs in being strongly clonal and long rhizomatous (versus rhizomes absent), and having shorter and more consistently opposite and decussate leaves. *Helianthus waccamawensis* also differs in achene scale morphology, having strongly deltoid to lanceolate scales 0.5 mm wide or greater compared to aristate scales less than or equal to 0.3 mm wide.

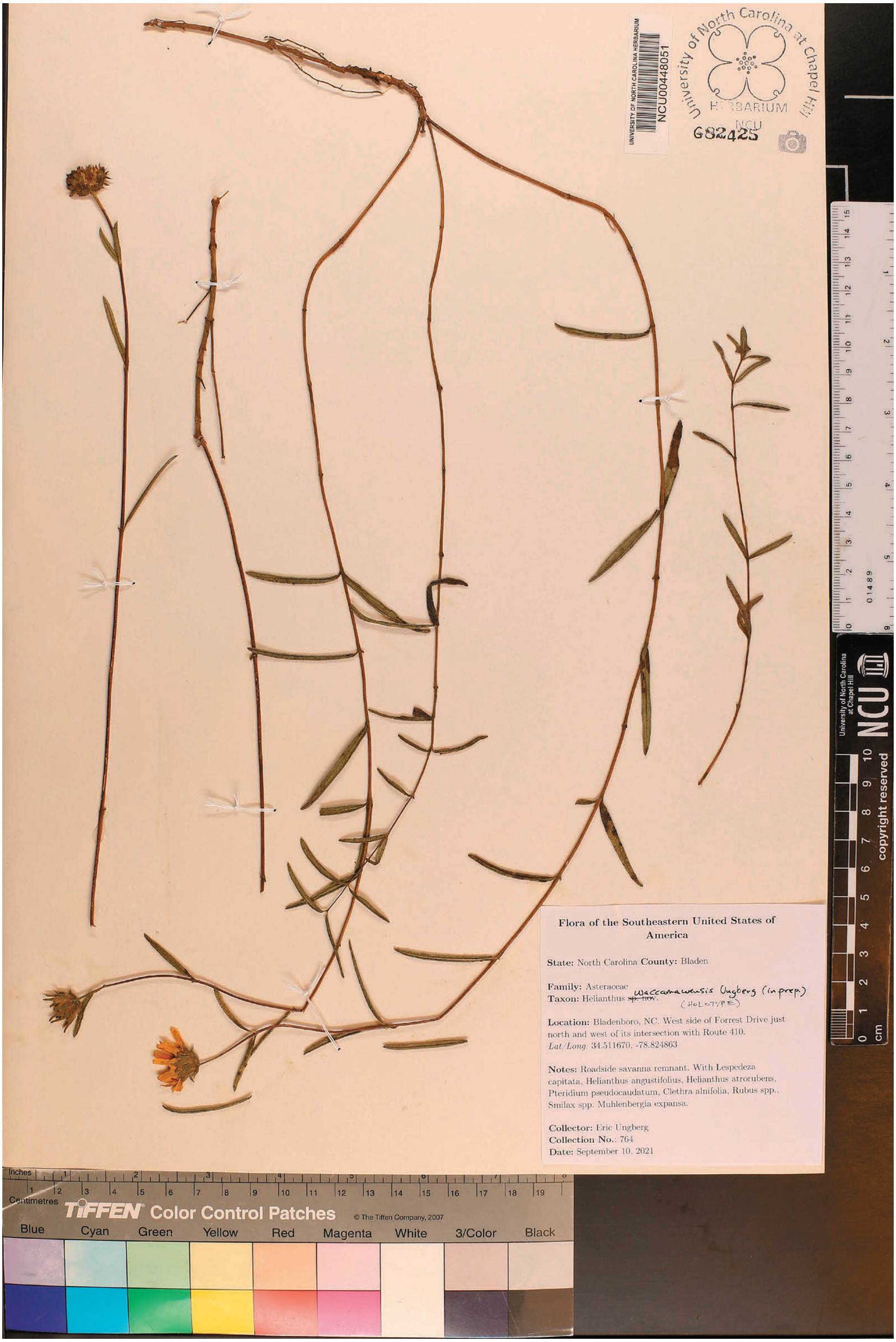
Description.—*Perennials:* 30–90 cm tall; rhizomatous and extensively colonial, lacking prominent crown buds and/or caudices. *Stems:* usually green to sometimes glaucous or darkened at the nodes, hispid to strigose with ascending to appressed hairs. *Leaves:* lacking basal leaves or rosettes; cauline usually opposite, sometimes becoming alternate distally; sessile or nearly so; blades 1-nerved (lowest stem leaves often 3-nerved), linear to linear lanceolate; margins ± parallel and revolute; adaxial surface harshly scabrous, abaxial surface gland-dotted and with prominent trichomes; averaging 5–10× longer than wide at mid-stem on living plants, sometimes narrower on herbarium specimens; usually with several pairs of prominent marginal cilia near base. *Heads:* usually 1–3, robust or damaged stems occasionally with up to 9. *Peduncles:* 1–5(–10) cm. Involucres: 8–20 mm in diameter; hemispheric or turbinate to slightly cylindrical. *Phyllaries:* 20–40; oblanceolate to lanceolate, with apices acute to obtuse; apices of outer phyllaries somewhat thick in texture; abaxial faces strigose, gland dotted distally; margins prominently ciliate, especially basally. *Paleae:* 7–9 mm; conduplicate and slightly keeled abaxially; obviously nerved; apices entire, acute, and usually ciliate. *Ray florets:* Usually about 13, though deciduous and often appearing to have fewer; laminae 15–35 mm long; abaxial faces sparsely pilose along veins, sometimes sparsely gland-dotted; surfaces distinctly papillate. *Disc florets:* 30–70, corollas 4.5–6(–7) mm long, lobes yellow and usually >1 mm. *Cypselae:* 3.0–5.0 mm in length; with two deltoid to lanceolate pappus scales (often with additional reduced scales of irregular shape); usually densely hairy at the summit and along margin. Ploidy: $2n = 6x = 102$ (hexaploid).

Phenology.—Peak flowering typically occurs in early September. It has been observed with fully developed flowers as early as August 1 (2024) in cultivation, and August 16 (2024) in the wild. In three years of field observations, *Helianthus waccamawensis* consistently flowers prior to *H. angustifolius* where the two species are sympatric, and has mostly finished flowering by the time *H. angustifolius* is just beginning (E. Ungberg, pers. obs.).

Etymology.—This new species is named for Lake Waccamaw and the Waccamaw Siouan Tribe, whose lands occur over parts of Columbus and Bladen counties in southeastern North Carolina. The majority of historic collections and currently known extant populations of this species have come from this area.

Common Name.—We propose Waccamaw Sunflower as a suitable common name.

Additional specimens examined. **U.S.A. NORTH CAROLINA. Bladen Co.:** disturbed savannah, Rt. 211 right-of-way, ca. 1 mi SE of Council, 28 Aug 1948, *Fox 1862* (NCSC, BRY); longleaf pine savanna, 4 mi SE of Bladenboro, 28 Aug 1949, *Fox 3296* (NCSC); savannah strip along railroad, 1 mi SE of Richardson on NC 211, 3 Aug 1957, *Ahles 33303* (NCU); powerline mesic savanna association along SR 1171 0.5–0.6 mi E of SR 1172, 16 Oct 2003, *LeBlond 5855* (NCU); Broad powerline E of Rosindale Road, S of NC 211, 30 Jul 2004, *Sorrie 11334* (NCU); Rosindale longleaf pine forest, around base of poles in powerline corridor 0.25 mi ESE of SR1708 and 0.2 mi S of NC 211, 13 Sep 2004, *LeBlond 6017* (NCU); S side of Old Lake Road/Route 1740, just W of its intersection with Moore's Lane Road, boundary of pine plantation and agricultural field, 10 Sep 2021, *Ungberg 760* (NCU); S side of State Route 211 ca. halfway between its intersections with Susie Baldwin and Everett Byrd Roads, Emerson, 10 Sep 2021, *Ungberg 759* (NCU); N side of Sarah Peterson Road, ca. 0.25 mi E of its intersection with Rosindale Road, Council, 10 Sep 2021, *Ungberg 768* (NCU); in power-line right-of-way on both sides of Route 211, ca. 0.4 mi SE of its



Flora of the Southeastern United States of America

State: North Carolina **County:** Bladen

Family: Asteraceae
Taxon: Helianthus ~~sp. nov.~~ waccamawensis Ungberg (in prep.)
(HOLOTYPE)

Location: Bladenboro, NC. West side of Forrest Drive just north and west of its intersection with Route 410.
Lat/Long: 34.511670, -78.824863

Notes: Roadside savanna remnant. With Lespedeza capitata, Helianthus angustifolius, Helianthus atrorubens, Pteridium pseudocaudatum, Clethra alnifolia, Rubus spp., Smilax spp. Muhlenbergia expansa.

Collector: Eric Ungberg
Collection No.: 764
Date: September 10, 2021

Fig. 7. Holotype specimen of *Helianthus waccamawensis*, NCU00448051. Collected by first author 10 Sep 2021 in Bladen Co., North Carolina, U.S.A.

intersection with Elwell Ferry Road, Council, 10 Sep 2021, *Ungberg 769* (NCU); E side of State Route 131, ca. 0.6 mi NNW of Grace Baptist Church, Bladenboro,19 Sep 2021, *Ungberg 829* (NCU); E side of Twisted Hickory Road, ca. 0.85 mi S of its intersection with Grimsley Farm Road, Abbotts Township, 19 Sep 2021, *Ungberg 830* (NCU); E side of Grimsley Farm Road on either side of powerline right-of-way crossing, Abbotts Township, 3 Oct 2021, *Ungberg 828* (NCU). **Brunswick Co.:** regularly mowed strip between railroad and fire-suppressed wet pine flatwoods, Leland, 21 Oct 2019, *Jackson s.n.* (NCU). **Columbus Co.:** near Bug Hill, 26 Aug 1927, *Schallert 9449* (DUKE); sandy places, Nakina, 18 Oct 1934, *Schallert s.n.* (NCU); roadside wood border near stream at Old Dock, 29 Aug 1938, *Godfrey 6323* (IND); ca. 5 mi S and 2 mi E of Chadbourn, 26 Aug 1979, *Gershenzon 57* (TEX); proceed 5 mi N of Lake Waccamaw to St. James Baptist Church, go E 0.2 mi then N 0.4 mi on dirt road on sandy edge of old field, 5 Sep 1980, *Gershenzon 148* (TEX); Livingston Chapel Road just NW of its intersection with State Route 1833, on S side of road, 19 Sep 2021, *Ungberg 831* (NCU); SW side of 7 Creeks Highway, ca. 300 feet SE of Zion Plain Missionary Baptist Church, Bug Hill, 3 Oct 2021, *Ungberg 827* (NCU); along S side of Old Lake Road E of its intersection with Buckhead Road, Bolton Township, 3 Oct 2012, *Ungberg 826* (NCU). **SOUTH CAROLINA. Horry Co.:** Conway, 1 Sep 1940, *Schallert s.n.* (GH); Savanna and Carolina bay complex near Floyds and Mossy Bay, 3 Aug 1983, *Pinson 706* (CCUH).

REVISED KEY TO SELECTED *HELIANTHUS* OF THE SOUTHEASTERN UNITED STATES

This key begins at couplet 22 of Helianthus Key D in Weakley & Southeastern Flora Team (2024), or (with slight alterations) couplet 64 of the Flora of North America *Helianthus* treatment (Schilling 2006). Note that when keying plants based strictly on vegetative features, hybrids of *H. angustifolius* and *H. floridanus* may superficially resemble the largest individuals of *H. waccamawensis*. Achene and floral characters (Table 1) reliably separate *H. waccamawensis* from *H. floridanus*, *H. angustifolius*, and their hybrids. It is also important to note that hybrids of *H. floridanus* and *H. angustifolius* are not found in the region where *H. waccamawensis* occurs.

1\. Heads relatively small, discs usually <15 mm across; abaxial leaf surfaces softly pubescent (on living plants, excepting the scabrous leaf margins and midvein); tubers present [of the Piedmont in SC and NC] **Helianthus schweinitzii**

1\. Heads various in size (8–20 mm+); abaxial leaf surfaces various but not softly pubescent; tubers absent [collectively widespread]

  2\. Leaf margins conspicuously undulate, leaves narrowly lanceolate to ovate, mostly 3-veined (at mid-stem); inflorescences mostly 1–6 heads; plants rhizomatous; achene pappus scales aristate [wet habitats, southern SC and southward] **Helianthus floridanus**

  2\. Leaf margins not conspicuously undulate, leaves linear to lanceolate, mostly with a single prominent main vein (at mid-stem, lowest leaves may be 3-veined); inflorescences with few (1) to many (16+) heads; plants rhizomatous or not; achene pappus scales aristate or not [habitats various, collectively widespread]

    3\. Plants robust, >1.5 m tall; leaves >1 cm wide; rhizomatous **Helianthus simulans**

    3\. Plants shorter, <1.5 m tall; leaves <1 cm wide; rhizomatous or not.

      4\. Plants <1 m tall at maturity, strongly rhizomatous; mid-stem leaves <6(–10) cm long, mostly opposite; inflorescences of usually 1–3(–10) heads; disc florets yellow; achene pappus scales deltoid to lanceolate (usually ≥0.5 mm wide and 1-4× as long as wide), often with additional irregularly shaped scales [Cape Fear Arch region of NC and SC] **Helianthus waccamawensis**

      4\. Plants usually >1 m tall at maturity, not rhizomatous, from crowns or caudices; mid-stem leaves 8–20 cm long, alternate or opposite; Inflorescences of usually 3–16(–many) heads; disc florets yellow or red to purple; achene pappus scales narrowly lanceolate to aristate (0.1–0.3 mm wide and ≥7× as long as wide), lacking additional irregularly shaped scales [widespread] **Helianthus angustifolius**

Habitat and Distribution.—*Helianthus waccamawensis* is restricted to four contiguous counties in southeastern North Carolina (Bladen, Brunswick, and Columbus cos.) and northeastern South Carolina (Horry Co.). Figure 2 shows the respective ranges of *H. waccamawensis* and *H. floridanus* in North and South Carolina. The range of *H. waccamawensis* is, therefore, the "island" of upland habitats delimited by a combination of Big Swamp, Lumber River, and Little Pee Dee River to the west, the Cape Fear River to the north and east, and the Waccamaw River to the east and south.

Most populations of *H. waccamawensis* occur in savanna remnants associated with roadsides and powerline rights-of-way that, through light mechanical disturbances such as mowing, prevent encroachment by taller woody vegetation and thereby mimic the sunny, open conditions historically maintained by periodic fire. Cartwheel Bay Heritage Preserve in South Carolina contains perhaps the best example of *H. waccamawensis* occurring in a high-quality natural community (Fig. 8). Associates there include *Pinus palustris* P. Miller, *P. taeda* L., *Quercus elliottii*, *Quercus falcata* Michx., *Quercus marilandica* Münchh., *Clethra alnifolia* L., *Ilex glabra* (L.) A. Gray, *Lyonia mariana* (L.) D. Don, *Symplocos tinctoria* (L.) L'Hér., *Vaccinium tenellum* Aiton, *Ageratina aromatica* (L.) Spach, *Aristida stricta* Michx., *Arundinaria tecta* (Walter) Muhl., *Asclepias michauxii* Decne.,

Fig. 8. Mesic pine savanna community at Cartwheel Bay Heritage Preserve in Horry Co., South Carolina. A single flowering stem of *H. waccamawensis* can be seen in the foreground.

Balduina uniflora Nutt., *Eryngium yuccifolium* Michx. var. *synchaetum* A. Gray ex J.M. Coult. & Rose, *Eupatorium leucolepis* (DC.) Torr. & A. Gray, *Eupatorium rotundifolium* L., *Eurybia paludosa* (Aiton) G.L. Nesom, *Gentiana autumnalis* L., *Gymnopogon brevifolius* Trin., *Lespedeza capitata* Michx., *Pteridium pseudocaudatum* (Clute) Christenh., *Solidago odora* Aiton, *Solidago tortifolia* Elliott, *Symphyotrichum walteri* (Alexander) G.L. Nesom, *Trilisa paniculata* (J.F. Gmel.) Cass., and *Xyris caroliniana* Walter. The canopy is relatively open, and the shrub layer, though dense in places, remains low in stature due to periodic prescribed fire. The herb layer is diverse but dominated by *Aristida stricta*.

The preferred habitats of *H. waccamawensis* differ from those of *H. floridanus* and *H. angustifolius*. Although *H. angustifolius* often co-occurs with *H. waccamawensis*, it generally tolerates a broader range of hydrological conditions and soil types and frequently extends into wetter habitats. Similarly, *H. floridanus* is nearly always found in wetlands, occurring in "wet savannas and pocosin edges" according to Weakley and the Southeastern Flora Team (2024) and "wet woods, bogs, and swales in the Coastal Plain" according to NatureServe. Other sources, such as Godfrey and Wooten (1981) and Wunderlin and Hansen (2011), provide similar descriptions of *H. floridanus* as occupying wet habitats, and the USDA lists its wetland indicator status as facultative-wetland, meaning that it occurs predominantly in wetlands. In contrast, *H. waccamawensis* occurs in more mesic niches where soils are rarely saturated, and few obligate wetland species are found.

In the Classification of the Natural Communities of North Carolina (Schafale 2023), the communities inhabited by *H. waccamawensis* generally correspond most closely to the Mesic Pine Savanna Lumbee Subtype. The Lumbee Subtype is listed as occurring in Robeson Co. and nearby areas in the inner coastal plain. The Lumbee Subtype is distinguished from other Mesic Pine Savanna Subtypes by the presence of *Quercus elliottii* Wilbur, which is rare and state-endangered in North Carolina (Wichmann & Wojcik 2022). *Helianthus floridanus* (in actuality, *H. waccamawensis*) is listed as one of the rare species associated with the Lumbee Subtype. The community description of the Lumbee Subtype thus seems clearly meant to correspond to several locales where both species co-occur in southwest Bladen County. While *H. waccamawensis* does often co-occur with *Q. elliottii*, the latter species' utility as a unique identifying feature of the Lumbee Subtype of Mesic Pine Savanna likely diminishes moving away from Robeson County. *Quercus elliottii* becomes much more common to the east and south, especially in South Carolina, where it can be found in a far greater variety of mesic habitats, including those where *Amorpha confusa* (Wilbur), S.C.K. Straub, Sorrie, & Weakley occur, which is considered as occurring in the Coastal Plain Subtype of Mesic Pine Savanna (Schafale 2023). Populations of *H. waccamawensis* further south and east may, therefore, grade into communities more closely resembling the Coastal Plain Subtype of Mesic Pine Savanna, or it may be that the Lumbee Subtype ranges more widely than previously thought. A third possibility is that there is a novel Mesic Pine Savanna community occurring in this area that has yet to be described. Few intact examples of either the Lumbee or Coastal Plain Subtypes of Mesic Pine Savannas remain in the range of *H. waccamawensis*, with much of the mesic lands they occur over having been converted to agricultural uses (Schafale 2023). Both community types are considered rare both regionally and globally (Schafale 2023).

Mesic longleaf pine savannas and many of their associated species encompass a far greater range than that occupied by *H. waccamawensis*, making this species' restricted range somewhat puzzling. We hypothesize that the limited range of *H. waccamawensis* must be due, at least in part, to the presence of broad expanses of unsuitable bottomland habitat surrounding its core habitat, promoting its isolation. The lack of obvious modifications for dispersal and the relatively large and heavy achenes further suggest that the dispersal ability of *H. waccamawensis* is probably limited. Nevertheless, we hope that additional populations may be found beyond the range described here. In particular, areas in Robeson Co., NC, where *Q. elliottii* has been found should be prioritized for future surveys, though a review of all digitized *Helianthus* specimens from Robeson Co. on SERNEC did not reveal any additional occurrences of *H. waccamawensis*.

Conservation Ranking.—Following Faber-Langendoen et al. (2012), we establish (or propose) NatureServe global, national, and state conservation ranks for *H. waccamawensis* and state ranks for *H. floridanus*. Conservation ranks were determined using the NatureServe Rank Calculator Version 3.2 (2020) in conjunction with the IUCN's GEOCAT online tool (Bachman et al. 2011). Rank calculations incorporated a high baseline level of threat for *H. waccamawensis* due to the precarity of most known populations and few known occurrences on protected lands.

The description of *H. waccamawensis* also has implications for the state (and potentially global) ranks for *H. floridanus*. In the course of searching for additional records of *H. waccamawensis*, all of the most northern records of *H. floridanus* were examined. A specimen of *H. floridanus* from Robeson County, NC (NCU00087780) is incomplete but is likely *H. simulans*, which was observed escaping from cultivation at several sites less than a kilometer from the collection locale. We failed to relocate the population despite two attempts. The rank of S1 in North Carolina is, therefore, no longer applicable, as the species does not occur in the state. A specimen from Clarendon County, South Carolina (NCU00053479) is correctly identified, but several attempts to relocate this population have failed, and it is considered extirpated. The remaining two most northern specimens of *H. floridanus*, from Williamsburg (FMUH0001848) and Darlington (FMUH0004626) Cos., South Carolina, are misidentified and represent *H. heterophyllus* and *Coreopsis grandiflora* Hogg ex Sweet, respectively. The previous rank of SNR in South Carolina has been updated by the South Carolina Heritage Trust to S1, reflecting its rarity in the state. *Helianthus floridanus* can now be considered to range from Louisiana, across the Gulf Coastal Plain, throughout much of the northern half of Florida, and north along the Atlantic Coastal Plain to southeastern South Carolina (Kartesz 2015). Given our proposed (NC) and actual (SC) revisions of these two state ranks, it may be appropriate to revise the global rank of G3G4 (presumably downward) to reflect the more restricted range of *H. floridanus*.

For *H. waccamawensis*, we recommend a state rank of S2 in North Carolina and have assigned a state rank of S1 in South Carolina. The existing rank of S1 for *H. floridanus* in North Carolina is no longer applicable to *H. waccamawensis* because we documented twelve previously unknown populations during fieldwork for this study. We also calculated global and national ranks of G2 and N2 for *H. waccamawensis*. NatureServe considers G2-ranked species as being "Imperiled: At high risk of extinction or collapse due to restricted range, few populations or occurrences, steep declines, severe threats, or other factors."

Threats to *H. waccamawensis* are numerous. Nearly all populations occur in roadside habitats that are vulnerable to associated management activities such as herbicide treatments or mowing, the timing of which might negatively affect its ability to sexually reproduce. In 2023, one population in Bladen Co. was observed to have been greatly reduced in size due to recent herbicide treatments (E. Ungberg, pers. obs.). Though much of its historic habitat has already been altered or destroyed following the conversion of the greater southeastern longleaf pine ecosystem to agricultural and silvicultural uses, high rates of human population growth in the area forecast further development of this already imperiled ecosystem. Two of the four counties it is known to occur in have the highest (Brunswick Co.) or second highest (Horry Co.) rates of human population growth in their respective states. Increased development may impact even protected populations, such as reducing the ability of land managers to conduct prescribed burns, due to concerns about air quality or fire containment.

Gaps in our current knowledge of *H. waccamawensis* may obscure additional threats to this species. We lack basic demographic data and have, at best, only qualitative estimates of population sizes. Additionally, we lack data on population-level demographic trends, leaving us uncertain as to which populations are stable, increasing, or declining. Herbivory has been shown to negatively impact the long-term persistence of populations in other rare sunflowers (England 2017). The genetic structure of populations remains unknown. Given the strongly clonal growth habit of *H. waccamawensis*, even large populations may consist of few genetically unique individuals, a scenario that Fox et al. (2024) demonstrated to be present in the rare clonal species *Shortia brevistyla* (P.A. Davies) Gaddy and *Sagittaria fasciculata* E.O. Beal. Like many of the heliophytic species endemic to the longleaf pine ecosystem, we assume that *H. waccamawensis* benefits from periodic fire, but the extent to which fire frequency, intensity, and seasonality may affect its survival is unknown.

We hope that the publication of *H. waccamawensis*, a charismatic new sunflower and narrowly endemic species, will spur further research into its life history, ecology, and evolution. The unique plant species and communities found in the Cape Fear Arch region are of significant biodiversity importance both regionally and globally, and we are optimistic that the naming of this species will enhance awareness of native plant species and promote conservation opportunities.

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BOOK REVIEW

Robert Jensen, ed. 2023. **FROM THE GROUND UP, conversations with Wes Jackson.** (ISBN-13: 978-1-5179-1390-4, pbk; 978-1-73541-365-5, pbk). New Perennials Publishing, Editor, Bill Vitek, Director, the New Perennials Project; Scholar in Residence, Middlebury College, Professor Emeritus, Clarkson University. (**Orders:** https://www.newperennialspublishing.org/). free download, 72 pp., 6" × 9".

Foreword by Linda Ronstadt. The book narrative is a series of five conversations with Wes Jackson. Questions are posed and Jackson answers. The First Conversations is about *Intellectual Grounding* that focuses on his schooling beginning with a two-room rural school house to his doctorate in genetics. He tries to dispel the notion he is a genius but his thinking about the importance of soil and conservation issues has always been "outside the box." There is an appreciation of growing up on a farm in rural Topeka, Kansas, and the importance of a work ethic. This topical section is worth reading to appreciate the beauty of the tallgrass prairie landscape in the Flint Hills of Kansas.

The Second Conversation is *Respecting Your Tools*. Educational experiences mostly at Kansas Wesleyan University, University of Kansas, Sacramento State University in California and establishing The Land Institute highlight this phase of Wes Jackson's life story. Wes had always been a builder with his hands, tools, and a sense of place that resulted in building his home and outbuildings that eventually resulted in The Land Institute.

Conservation Three, *Mad About Science*. Here one learns science does not have all the answers to complex social problems. Science fails to ask hard questions about technological fixes in our modern world. The four pages of color plates show former activities and building and grounds since The Land Institute was established in the early 1970s. This section includes an explanation of crop diversity and species diversity and the importance of perennial polycultures versus monocultures of wheat, corn, and soybeans found on modern farms of today. This harkens back to the 1930s and his parents truck farm that produced 25 different vegetables that were grown for consumption and sale.

Conversation Four, *Methodism to My Madness*, or why is Wes a 5/8s Christian. This section of the book will test your belief system. Wes grew up in the Methodist church, taught Sunday school, asked the tough questions about religion and church doctrine and teachings in the Bible. His short section on the Nicene Creed is worth reading to get his assessment of the contents.

Conversation Five, *The Portrait of an Artist as an Old Man*. Here Wes discusses the importance of scrapyards, junkyards, and creativity. It will make you think about how to build things without much money. The last sentence of the book is something to ponder, "We can't avoid being participants in creating the Creation."

About the authors:

Quoted from the book. "**Wes Jackson**, is cofounder and president of The Land Institute in Salina, Kansas. He is the author and editor of numerous books, including *Hogs Are Up Stories of the Land with Digressions* and *New Roots for Agriculture*. **Robert Jensen** is professor emeritus in the School of Journalism and Media at the University of Texas at Austin. He is the author of many books, including *The Restless and Relentless Mind of Wes Jackson: Searching for Sustainability and Plain Radicals: Living, Loving, and Learning to Leave the Plant Gracefully*. Jackson and Jensen."

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