STUDIES ON BIGELOWIA (ASTEREAE, COMPOSITAE). 1. MORPHOLOGY AND TAXONOMY[1]

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INTRODUCTION

The genus *Bigelowia* (the rayless goldenrods) was established by DeCandolle in 1836, but the orthographic variant *Bigelovia* was generally used for the next 50 years. The genus as presently recognized contains only two species, both native to southeastern United States, but historically all species of *Chrysothamnus*, many of *Haplopappus*, and one each of *Solidago* and *Eupatorium* were included. Gray (1873), in his commentary on Bentham and Hooker's treatment of Compositae in Genera Plantarum (1873), retained the wide generic limits for *Bigelowia* but pointed out that those taxa referrable to Nuttall's *Chrysothamnus* were more akin to *Haplopappus* than to the original *Bigelowia*; they, in turn, were more like *Solidago*, section *Euthamia*. Recent studies (Shinners, 1951; Kapoor and Beaudry, 1966) support the generic distinctness of *Euthamia*.

In 1895, Greene argued for the re-establishment of *Chrysothamnus* for the rabbitbrushes and followed Britton's (1894) adoption of Rafinesque's name *Chondrophora* for the rayless goldenrods, since *Bigelowia* DC. was untenable as a later homonym. He also suggested that if *Chrysothamnus* and *Chondrophora* (*Bigelowia*, sensu stricto) were closely related, then his genus *Petradoria* would be intermediate in the relationship.

The name *Bigelowia* DC. was conserved for the rayless goldenrods at the Sixth International Botanical Congress of Amsterdam in 1935 (Camp et al., 1947). The generic name *Bigelowia* Rafinesque was rejected, and *Chondrophora* became a synonym.

METHODS AND MATERIALS

Morphological features of all available material were studied; however, several collections representing the geographical range for each taxon were selected and studied in great detail (cf. Table 2). References to measurements in the morphology section of this paper are based on that group of specimens.

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Measurements for vegetative features were from the largest of each unit (e.g., stem or leaf length or cauline leaf number) for each collection. Determining the average length of the several basal leaves per plant would be more difficult than measuring the longest and, therefore, probably less accurate for comparisons among the taxa. Average measurements for floral features were obtained as outlined in Anderson (1964).

Materials were borrowed from appropriate herbaria, collected by me in the field, or supplied by colleagues. The following are gratefully acknowledged for sending living specimens or seed: C. R. Bell, A. Clewell, R. K. Godfrey, S. B. Jones, O. Lakela, R. Lonard, S. F. McDaniel, and J. W. Thieret. T. M. Barkley is thanked for suggestions made on the manuscript, and L. H. Shinners for the Latin diagnoses.

MORPHOLOGY

Bigelowia nuttallii ("*B. virgata*") has been known to biology for over 150 years, but it has been infrequently collected and poorly understood (as is much of the southeastern flora; see Duncan, 1953). Many botanists, following Torrey and Gray (1842) and Britton (1894), have considered it simply as a narrow-leaved variety of the widespread *B. nudata*. It was also distinguished by its rather restricted habitat preference (Harper, 1906b, 1911; Brown, 1945). When grown in the greenhouse in several different soil mixtures over a period of years, *B. nuttallii* maintains its distinctive foliage. Actually, the two species are distinct in several aspects of morphology. Their distinctness is also indicated by anatomical and cytological studies in progress. There is, however, infraspecific variability in *B. nudata*; a new subspecies, *B. n.* subsp. *australis*, is described in this paper.

Vegetative morphology. Averages for major diagnostic features are summarized in Table 1 for the three entities; the ranges of variability for those features are reported in the systematic treatment. Additional comments are made in the text.

Rhizomes and short, narrow caudices characterize *B. nuttallii*; whereas plants of *B. n.* subsp. *nudata* are cespitose with a short, stocky caudex up to 10 mm wide. Occasionally, layering by sediments results in an elongated, rhizome-like caudex. In *B. n.* subsp. *australis*, conditions are intermediate: caudices are elongate, only moderately thickened, and frequently connected by short rhizomes.

Average stem height of *B. n.* subsp. *australis* is intermediate to that of the other taxa; however, extremes for the genus (86 and 22 cm) are found in this subspecies. Although stems of *B. nuttallii* are usually shorter than those of *B. nudata*, the former has more leaves. Distribution of cauline leaves warrants further attention because of the complex phyllotaxies present.

Leaf shape represents one of the more obvious differences among the taxa (Table I). Nevertheless, *B. nuttallii* from Texas can produce broadly spatulate leaves (up to 6.5 mm wide). In *Cory 50592* (SMU) and *Ripple 51-563* (KANU), the first basal leaves are typically linear, and the terminal ones of

TABLE 1. COMPARATIVE VEGETATIVE MORPHOLOGY IN BIGELOWIA (data represent averages of largest units)

Feature	*B. nuttallii*	*B. n. nudata*	*B. n. australis*
caudex length, cm	1.03	1.13	3.14
stem height, cm	39.5	59.2	48.3
stem leaf number	17.4	11.2	10.3
basal leaf length, cm	9.7	7.7	13.1
basal leaf width, mm	1.2	7.3	3.3
first stem leaf length, cm	7.1	5.0	9.5
first stem leaf width, mm	1.0	4.0	2.5
third stem leaf length, cm	5.7	3.4	5.2
third stem leaf width, mm	0.9	2.1	1.8

the rosettes are broad. *Anderson 3173* (KSC) produced spatulate leaves after being transplanted to a greenhouse in Manhattan, Kansas. Plants of the same population raised in the greenhouse from seed had the typically narrow leaves seen in the original field collection. In all plants of *B. nuttallii* with the broadened basal leaves, the cauline leaves are typically narrow, and features of the inflorescence are constant also. In all taxa basal leaves are frequently withered by flowering time; this is most pronounced in *B. n. australis*.

Floral morphology. Data for floral features are compiled in Table 2. Those for selected taxa of *Euthamia* are listed in Table 3 for comparison; for *Petradoria*, see Anderson (1963).

Inflorescences are corymbose and flat-topped in the rayless goldenrods. Those of *B. nuttallii* are noticeably smaller. Using measurements of the longest inflorescence branch for each collection of Table 2, the following averages are derived: *B. nuttallii*, 8.5 mm; *B. n.* subsp. *nudata*, 11.4; and *B. n.* subsp. *australis*, 10.8.

Heads of *B. nuttallii* are relatively narrower than those of *B. nudata*. The width/length ratio for involucres of *B. nuttallii* averages 0.26, but averages 0.34 for *B. nudata*.

Individual involucral bracts of *B. nuttallii* are narrower than those of *B. nudata*. The bracts are often aligned vertically, but the alignment varies greatly within each taxon. For example, in *B. n.* subsp. *australis* they are strongly aligned in *Godfrey 65642* (FSU), weakly so in *Small & Carter 1026* (NY), but not at all in *Kral 3949* (FSU). Such variation is contrary to the statement by Hall and Clements (1923, p. 157) that there is no tendency for involucral bracts to form vertical rows in *Bigelowia*.

The receptacle is either alveolate or with a central cusp similar to that frequently found in *Petradoria* (Anderson, 1963) or the setaceous receptacle characteristic of *Euthamia* (Table 3). As in *Petradoria*, the geographic occurrence of such a receptacle in the rayless goldenrods is sporadic.

TABLE 2. AVERAGED DATA FOR SELECTED FLORAL FEATURES IN BIGELOWIA

taxon and collection data	*bract number*	*involucral length, mm*	*involucral width, mm*	*receptacular cusp, mm*	*flower number*	*corolla length, mm*	*corolla lobe length—total length, %*	*stigmatic area—total style branch, %*
B. nuttallii								
GEORGIA: Washington Co.: 3 mi N Harrison, *Pyron & McVaugh 3094* (GA)	11.8	6.7	1.6	0.48	3.7	4.1	33.3	64.8
GEORGIA: Coffee Co.: "The Rocks," 8 mi N Broxton, *Montgomery 1052* (GA, KSC)	12.5	7.1	1.8	0.52	3.2	5.1	35.6	58.9
GEORGIA: Turner Co.: 6 mi S Arabi, *Anderson 3089* (KSC)	11.0	7.5	1.4	0.42	3.0	4.2	31.9	59.7
GEORGIA: Rockdale Co.: 6 mi NE Conyers, *Pyron & McVaugh 1100* (GA, US)	16.2	6.8	1.8	0.86	3.5	5.0	36.1	58.1
FLORIDA: Washington Co.: Rock Hill, 4.5 mi SE Chipley, *Godfrey 63191* (FSU, KSC, NCU, USF)	13.2	6.6	1.5	0.92	3.0	3.9	30.4	54.1
ALABAMA: DeKalb Co.: Little River, 8 mi SE Fort Payne, *McDaniels 3930* (FSU, KSC)	12.5	6.1	1.7	0.59	4.2	4.1	36.3	56.9
ALABAMA: DeKalb Co.: Lookout Mtn., *Mohr 10* in 1892 (MO, NY, US)	14.7	6.3	1.8	0.63	3.5	3.9	38.0	59.2
LOUISIANA: Jeff Davis Par.: Welsh, *Palmer 8508* (MO, NY, US)	14.7	7.5	1.9	0.59	4.0	—	—	—
LOUISIANA: Vernon Par.: SW Slagle, *Thieret 25200* (KSC)	14.8	7.6	2.2	0.48	3.8	4.6	38.2	59.0
LOUISIANA: Calcasieu Par.: Lake Charles, *Mackenzie 480* (KSC, MO, NY, US)	14.4	7.5	1.9	0.51	4.4	4.4	33.7	56.9
LOUISIANA: Sabine Par.: 5 mi S Florien, *Thieret 20775* (DUKE, FSU, GA)	19.4	7.4	1.9	0.46	4.0	4.4	26.5	59.8
TEXAS: Newton Co.: 5 mi E Kirbyville, *Cory 49800* (GH, NY, SMU, TAES, US)	13.5	7.8	2.1	0.46	3.0	4.9	34.5	57.1
TEXAS: Brazoria Co.: Chocolat Bayou, *Lindheimer 86* in 1843 (GH, MO)	16.5	8.4	1.9	0.59	4.3	5.3	25.6	64.4
TEXAS: Austin Co.: *Tharp 44281* (KSC, MO, TEX)	15.1	8.4	2.3	0.34	4.0	5.1	28.0	55.8
TEXAS: Brazos Co.: Minter Springs, SW Wellborn, *Anderson 3173* (KSC)	17.2	9.0	2.3	0.57	4.9	5.3	29.2	61.4
TEXAS: Brazos Co.: Bryan, *Palmer 10735* (MO, US)	23.8	7.7	2.1	0.59	4.8	—	—	—
B. nudata ssp. *nudata*								
NORTH CAROLINA: Dare Co.: Roanoke Island, 2 mi S Manteo, *Godfrey & Fox 51041* (DUKE, FSU)	13.6	5.0	1.8	0.70	4.0	3.7	34.8	68.0
NORTH CAROLINA: Martin Co.: 4 mi SSE Smithwick, *Radford 41801* (NCU)	13.2	4.6	1.8	0.59	4.2	3.6	29.9	60.3
NORTH CAROLINA: Hyde Co.: 3.2 mi E Leechville, *Radford 42646* (NCU)	11.8	5.5	1.8	1.26	3.2	4.1	33.6	65.1
NORTH CAROLINA: Onslow Co.: 8 mi SW Jacksonville, *Godfrey 6450* (NCU, NY)	11.3	4.7	1.7	0.34	3.5	3.4	32.9	63.2

taxon and collection data	*bract number*	*involucral length, mm*	*involucral width, mm*	*receptacular cusp, mm*	*flower number*	*corolla length, mm*	*corolla lobe length—total length, %*	*stigmatic area—total style branch, %*
NORTH CAROLINA: Robeson Co.: 6 mi NE Lumberton, *Fox 5590* (FSU, GH)	13.0	4.7	1.8	0.70	4.3	3.6	27.5	59.7
NORTH CAROLINA: New Hanover Co.: Wilmington, *Smith 14367* (MO)	12.2	4.9	1.8	0.34	4.0	3.6	30.7	61.8
SOUTH CAROLINA: Horry Co.: Conway, *Grace* in 1940 (GH, MO)	10.3	5.7	1.7	0.42	3.3	3.9	29.8	61.5
SOUTH CAROLINA: Georgetown Co.: 5 mi S Georgetown, *Godfrey 8122* (DUKE, MO, NY, US)	15.7	5.8	2.1	0.17	4.7	3.9	32.6	60.0
	14.8	8.6	2.2	0.48	3.8	4.6	38.2	59.0
SOUTH CAROLINA: Orangeburg Co.: Eutawville, *Eggleston 5003* (GH, MO, NY, US)	11.6	5.8	1.8	1.25	3.8	4.0	29.8	63.0
SOUTH CAROLINA: Bamberg Co.: 2.5 mi S Denmark, *Ahles 37586* (NCU)	10.6	5.1	1.8	0.21	3.6	3.6	29.4	63.2
GEORGIA: McIntosh Co.: 2 mi NE Ft. Barrington, *Bozeman & Radford 2318* (NCU)	12.8	5.2	1.7	0.79	3.0	3.6	34.9	64.2
FLORIDA: Duval Co.: Jacksonville, *Curtis 1356* (GA, GH, KANU, MO, NY, SMU, US)	15.5	5.9	1.8	0.55	3.3	4.2	36.5	65.8
FLORIDA: St. John's Co.: Orangedale, *Moldenke 164* (DUKE, MO, NY)	16.5	6.0	1.8	1.11	3.7	3.8	30.6	66.7
FLORIDA: Alachua Co.: 2.5 mi W Hawthorne, *Ward 3567* (DUKE, GA, NCU, SMU, USF)	15.2	5.6	1.8	0.81	4.0	3.8	37.0	64.9
GEORGIA: Lowndes Co.: Valdosta, *Huger* in 1913 (MO)	11.5	4.9	1.6	0.34	3.0	3.8	32.1	67.5
GEORGIA: Turner Co.: 6.5 mi S Arabi, *Anderson 3088* (KSC)	11.3	5.6	1.5	1.05	3.0	3.6	36.8	62.6
GEORGIA: Thomas Co.: 12 mi N Thomasville, *Godfrey 67434a* (FSU)	11.4	5.1	1.8	0.88	3.2	4.0	30.1	58.2
FLORIDA: Wakulla Co.: 3 mi S Newport, *Anderson 3070* (KSC)	12.6	4.8	1.6	0.70	3.3	4.0	36.2	61.1
GEORGIA: Grady Co.: 2 mi W Whigham, *Godfrey 63227* (FSU)	13.2	5.5	1.8	0.08	3.8	3.8	30.0	69.7
FLORIDA: Franklin Co.: Apalachicola, *Chapman 143b* (MO, NCU, NY, US)	12.8	4.9	1.8	0.80	3.5	3.6	34.7	60.8
FLORIDA: Washington Co.: Rock Hill, 4.5 mi SE Chipley, *Godfrey 63190* (FSU)	15.1	5.3	1.8	1.02	3.7	3.7	29.1	63.6
FLORIDA: Santa Rosa Co.: 4.5 mi E Gulf Breeze, *McDaniel 3864* (FSU)	15.4	6.1	1.7	0.67	3.0	3.9	26.9	62.0
ALABAMA: Baldwin Co.: Gateswood, *Tracy 8667* (MO, NY, US)	11.8	5.0	1.6	0.34	3.0	3.2	35.7	64.7
MISSISSIPPI: Jackson Co.: Ocean Springs, *Skehan 1345* (MO, NY, US)	14.0	5.0	1.9	1.30	4.0	3.6	28.7	61.0
MISSISSIPPI: Harrison Co.: Biloxi, *Tracy 4375* (KANU, MO, NY, SMU, US)	13.5	5.3	1.8	0.43	3.5	3.5	30.9	60.8
MISSISSIPPI: Forrest Co.: Hattiesburg, *Jones 11071* (KSC)	16.0	5.0	1.8	0.55	4.1	3.7	35.8	62.0
MISSISSIPPI: Pearl River Co.: Nicholson, *Kearney* in 1896 (NY)	14.4	5.6	1.6	0.96	2.6	3.6	34.9	61.1
LOUISIANA: St. Tammany Par.: Covington, *Hale s.n.* (KSC)	16.9	5.9	1.7	0.34	3.5	3.8	38.5	62.9

taxon and collection data	*bract number*	*involucral length, mm*	*involucral width, mm*	*receptacular cusp, mm*	*flower number*	*corolla length, mm*	*corolla lobe length—total length, %*	*stigmatic area—total style branch, %*
B. nudata ssp. *australis*								
FLORIDA: Pasco Co.: hiway 41, 2 mi N hiway 52, *Ray 9595* (FSU, USF)	14.8	6.8	2.2	0.85	4.0	4.4	33.9	62.8
FLORIDA: Pinellas Co.: Cross Bayou, *Barnhart 2774* (MO, NY)	13.0	6.6	2.4	0.81	5.2	5.0	36.4	63.0
FLORIDA: Pinellas Co.: 4 mi W St. Petersburg, *Deam 2841* (NY)	15.2	6.9	2.1	0.66	4.2	4.2	33.3	67.7
FLORIDA: Okeechobee Co?: Okeechobee region of Brevard Co. in 1903, *Fredholm 6155* (NY, US)	16.8	7.6	2.4	1.74	4.4	4.6	38.3	64.7
FLORIDA: Martin Co.: 6 mi W Stuart, *Godfrey 65642* (FSU)	17.0	6.8	2.3	0.79	4.0	4.4	32.9	62.1
FLORIDA: Martin Co.: 10 mi SE Sherman, *Kral 3949* (FSU, SMU)	16.3	6.9	2.3	0.72	5.0	4.5	36.1	69.1
FLORIDA: Lee Co.: 4 mi N Ft. Myers, *Godfrey 65376* (FSU)	19.2	7.2	2.4	1.16	4.2	4.8	32.4	64.5
FLORIDA: Lee Co.: Ft. Myers, *J. Standley 28* (GH, MO, NY, US)	14.0	6.0	2.3	1.10	5.3	5.0	31.0	67.0
FLORIDA: Lee Co.: Ft. Myers, *P. C. Standley 18886* (US)	14.8	6.8	2.2	0.38	3.6	4.4	36.1	76.0
FLORIDA: Collier Co.: west of hiway 29, Immokalee, *Anderson 3266* (KSC)	17.5	6.4	2.3	0.88	4.7	4.2	36.3	64.6
FLORIDA: Collier Co.: west of hiway 29, Immokalee, *Lakela 29408* (USF)	16.0	7.5	2.5	0.89	6.0	4.9	34.3	64.3
FLORIDA: Broward Co.: Fort Lauderdale, *Small & Carter 1026* (NY)	17.6	6.8	2.6	0.74	4.2	4.6	36.1	64.3
averages for *B. nuttallii*	15.1	7.4	1.9	0.56	3.8	4.6	32.7	59.0
averages for *B. nudata* ssp. *nudata*	13.3	5.3	1.8	0.67	3.6	3.7	32.5	63.0
averages for *B. Nudata* ssp. *australis*	16.0	6.9	2.3	0.89	4.3	4.6	34.8	65.8

TABLE 3. AVERAGED DATA FOR FLORAL FEATURES OF CERTAIN EUTHAMIA

Taxon and Collection	*Involucre*				*Ray flower*				*Disc flower*			
	bract number	*length, mm*	*width, mm*	*receptacular cusp, mm*	*flower number*	*corolla length, mm*	*limb length—total corolla length, %*	*limb width, mm*	*flower number*	*corolla length, mm*	*corolla lobe length—total length, %*	*stigmatic area—total style branch, %*
E. leptocephala												
Lonard 2008 (KSC)	20.6	5.4	2.1	1.03	10.2	3.5	50.0	0.21	3.6	3.8	34.0	52.2
Eggert in 1893 (KSC)	23.4	5.5	2.1	0.94	10.8	4.7	56.7	0.53	5.0	4.9	34.6	52.1
E. pulverulenta												
Lonard 2009 (KSC)	22.4	6.9	2.5	1.71	11.0	5.4	50.0	0.58	8.0	4.9	37.2	51.3
Cory 50667 (NY)	20.8	6.7	2.1	0.95	9.8	4.5	50.0	0.50	4.2	4.4	41.4	50.4
E. tenuifolia												
Boettcher 399 (KSC)	16.0	4.7	1.9	1.28	7.8	6.3	56.0	0.94	4.6	5.6	32.4	53.8
Heller 732 (KSC)	18.0	4.5	1.9	0.89	8.8	4.8	54.0	0.57	5.8	4.7	38.7	54.2
E. gymnospermoides												
Anderson 2600 (KSC)	27.0	7.6	1.9	0.67	12.5	5.2	53.7	0.50	3.1	4.5	34.7	32.5
E. nuttallii												
Anderson 2153 (KSC)	26.6	5.0	2.2	0.79	24.2	2.1	47.7	0.30	6.6	4.9	39.7	34.3
E. occidentalis												
Anderson 1488 (KSC)	17.6	5.8	3.2	1.07	18.2	4.7	50.7	0.50	9.0	4.4	33.7	46.3

Disc flowers are similar to those of *Euthamia* with corolla lobes recurved and about one-third the total corolla length; whereas those of *Petradoria* are only slightly spread and about one-fifth the total corolla length.

Style branches are subulate and included in the corolla of *Bigelowia* and *Euthamia*; they are narrow and exserted in *Petradoria* and *Chrysothamnus* (Greene, 1895). The ratio of stigmatic line to total style branch length in *B. nuttallii* approximates that of the *Euthamia* taxa (*E. leptocephala*, *E. pulverulenta*, and *E. tenuifolia*) from the same geographic area; those Euthamias from the central United States have obviously different ratios (Table 3).

Mature achenes are turbinate and sparsely pubescent. Those of *B. nuttallii* are the largest, averaging 3.2 mm long. They average 1.5 mm long in *B. n.* subsp. *nudata*, and 1.8 mm in *B. n.* subsp. *australis*.

Bigelowia shows considerable variability when features of floral morphology are compared to geographical distribution. Geographical ranking of collections was done along the long axis of the taxon's range (as listed in Table 2), i.e., from east to west for *B. nuttallii*, northeast to southwest for *B. n. nudata*, and north to south for *B. n.* subsp. *australis*. Significance of correlation was determined by Pearson's rank correlation test. Those floral features that showed correlation with geographical distribution are listed in Table 4. Achene size in *B. nuttallii* may be correlated with geography also. Those from Georgia average 3.0 mm long, whereas those from Texas average 3.4 mm.

Subspecies of *B. nudata* show no overall clinal variation. Paradoxically, a strongly pronounced cline exists for *B. nuttallii*. This species has a markedly discontinuous distribution (Fig. 1). One might argue that the discontinuity is rather recent because of the presence of the cline, but why then would *B. nudata* with its continuous distribution not have such a pronounced cline?

TAXONOMY

BIGELOWIA DC., Prodromus 5:326. 1836 [*nom. cons.*, see Camp, W. H., H. W. Rickett, and C. A. Weatherby. 1947. International rules of botanical nomenclature. Brittonia 6:1-120].

Chondrophora Raf., New Fl. N. Am. 4:79. 1838 [not 1836, as frequently reported, cf. Barnhart, J. H. 1907. The dates of Rafinesque's New Flora and Flora Telluriana. Torreya 7:177-181].

Suffrutescent herbs with leafy rosettes from a small caudex and fibrous roots; stems 3-7 dm tall, glabrous, viscid when young; leaves entire, linear to oblanceolate, minutely glandular punctate; cauline leaves progressively reduced in size and frequency, upper ones linear, shorter than the internodes; heads several in open, corymbose inflorescences; involucres cylindric, 4.5-9 mm high, phyllaries spirally arranged in ± vertical ranks, lanceolate, weakly keeled; receptacle alveolate or with a central cusp; disc flowers 2-6, yellow; corollas glabrous with strongly recurved lobes; style branches subulate; achenes turbinate or somewhat cylindrical, sparsely pubescent; pappus bristles dull white, capillary.

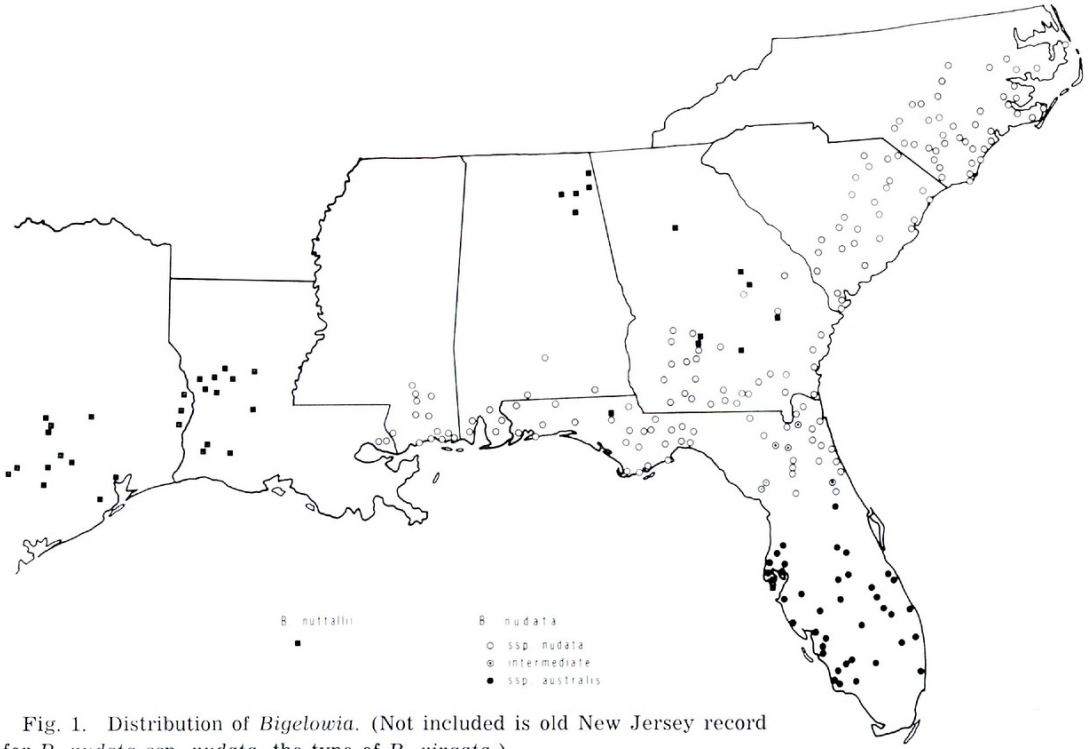

Fig. 1. Distribution of *Bigelowia*. (Not included is old New Jersey record for *B. nudata* ssp. *nudata*, the type of *B. virgata*.)

The genus consists of two species, *B. nudata* (type species) and *B. nuttallii*, from southeastern United States. It is closely allied to *Euthamia* in several aspects of morphology and appears to have similar ecological requirements. However, *Bigelowia* lacks ray flowers, hence the common name—rayless goldenrod. That distinction is not always a generic criterion; in fact, many species of Astereae have radiate and eradiate populations, e.g., *Chrysothamnus spathulatus* (Anderson, 1970). In addition, *Bigelowia* is distinct from *Euthamia* in habit; it has leafy basal rosettes and sometimes nearly scapose stems, whereas *Euthamia* has early-deciduous lower leaves and leafy stems.

A close relationship between *Bigelowia* and *Petradoria* was proposed by Greene (1895). He discounted the affinity of *Bigelowia* to *Euthamia* as suggested by Gray (1873) because "achenes in *Euthamia* are turbinate and silky." Greene apparently did not have adequate material, or he would have noted that achenes of *Bigelowia* are, in fact, turbinate and pubescent. Consequently, *Bigelowia* and *Petradoria* are dissimilar in their achenes as well as other morphological features (Anderson, 1963).

Affinity to *Chrysothamnus* (once considered part of *Bigelowia)* is not close.

Some observations have been made concerning phylogeny in *Bigelowia*. Harper (1911) suggested *B. nuttallii* might be a narrow-leaved extreme of *B. nudata*, developed in direct response to its rocky (drier) habitat. However, he preferred the alternative hypothesis—that *B. nudata* is the more recently derived and "being adapted to a widespread habitat became widely distributed."

Some features of the inflorescence of *B. nuttallii* such as larger, less numerous heads and larger flowers and seeds seem less specialized when compared with those of *B. nudata*. If *Bigelowia* is derived from *Euthamia*-stock, then rhizomaty in *B. nuttallii* might also be considered a primitive characteristic.

KEY TO THE TAXA

1. Plants definitely rhizomatous; all leaves narrowly linear, 1—2 mm wide (rarely more under cultivation) . . . . . 1. *B. nuttallii*

1. Plants cespitose or rarely weakly rhizomatous; lower leaves narrowly to broadly oblanceolate, spatulate or elliptic, 2—14 mm wide (*B. nudata*)

2. Basal leaves mostly less than 10 cm long, over 4 mm wide; flowers 3—4 mm long; heads 4.5—6.0 mm tall . . . 2a. *B. nudata* subsp. *nudata*

2. Basal leaves often over 10 cm long, less than 4 mm wide; flowers 4—5 mm long; heads 6.0—7.5 mm tall . . 2b. *B. nudata* subsp. *australis*

1. BIGELOWIA **nuttallii** L. C. Anderson, sp. nov. Perennis rhizomatosa (2.6) 3.5—5.0 (6.0) dm alta; folia basalia numerosa linearia (6) 8—12 (13) cm longa 1—2 mm lata, caulina 12—23 linearia infima 4.5—10.0 cm longa 1 mm lata; inflorescentia dense corymbosa plana; involucra 6.1—9.0 mm alta phyllariis 11—24; flores 3—5, corollae 3.9—5.3 mm longae lobis 1.2—1.6 mm;

linea stigmatica quam appendicula vix longior; achaenia 3.0—3.4 mm longa, pappus 4.0—4.4 mm longus.

Rhizomatous herbs with short narrow caudices; stems (2.6) 3.5—5.0 (6.0) dm tall; basal leaves numerous, linear (6) 8—12 (13) cm long, 1—2 mm wide; cauline leaves 12—23, linear, lowest ones 4.5—10.0 cm long, 1 mm wide; heads closely clustered in a flat-topped corymbose inflorescence; involucres 6.1—9.0 mm high, with 11—24 bracts; flowers 3—5, corollas 3.9—5.3 mm long, lobes 1.2—1.6 mm long; stigmatic line barely longer than style appendage; achenes 3.0—3.4 mm long; pappus 4.0—4.4 mm long (Fig. 1, squares).

Type: west bank, Ohoopee River, 3.5 mi W Reidsville, Tattnall Co., Georgia, at 100 ft. elevation, *Anderson 3455* (GA! KSC—holotype! NY! SMU! US!).

This is the plant which has long been known as *Bigelowia virgata* (Nutt.) DC. (or synonyms). The type locality of *Chrysocoma virgata* Nuttall however was New Jersey, far outside the range of the present species, but near the known modern limits of *B. nudata* subsp. *nudata*. A Nuttall collection (PH!; BM, photograph at KSC) labeled "*Chrysocoma virgata*, New Jersey" presumably is the type material. The PH sheet lacks basal parts; involucres average 5.3 mm long and corollas 3.5 mm long, the average involucral bract number is 15.2, all falling well in the range for *B. nudata* (see Table 2). Plants on the BM sheet (Fig. 2) have similar inflorescences and have basal parts of the plant intact; basal leaves are only 4 cm long and fully 11 mm wide.

Range: Locally established on sandstone or siltstone, usually confined to outcrops of Eocene to Pliocene strata from Georgia to eastern Texas. It is a characteristic species of the Altamaha Grit of Georgia, rock outcrops of the upper Oligocene studied extensively by Harper (1905, 1906b). Alabama populations are on sediments of the Carboniferous Period, and in Rockdale Co., Georgia, the plants occur on Lithonia Gneiss (Precambrian).

The species usually occurs on drier sites than *B. nudata*, but it grows along stream banks in northern Alabama well within reach of flood waters and also on rocks out in the streams (Harper, 1906a). Sept.—Oct.

Representative specimens: see Table 2; recently found in sandpine remnants in St. Petersburg, Pinellas Co., Fla., *Anderson 3464, 3468* (KSC), *Garrett s.n.* (FLAS).

2a. BIGELOWIA NUDATA (Michx.) DC. subsp. NUDATA, Prodromus 5: 329. 1836.

Chrysocoma nudata Michx., Fl. Bor. Am. 2: 101. 1803. "In humidis Carolinae," *André Michaux* (holotype P, photograph at KSC).—*Aster nudatus* (Michx.) Kuntze, Rev. Gen. 1: 318. 1891. — *Chondrophora nudata* (Michx.) Britton, Mem. Torrey Bot. Club 5: 317. 1894.

Bigelowia nudata var. *spathulaefolia* T. & G., Fl. N. Am. 2: 232. 1842. — *B. nudata* f. *spathulaefolia* (T. & G.) Gray, Proc. Am. Acad. Arts Sci. 8: 646. 1873.

Chrysocoma virgata Nutt., Gen. 2: 137. 1818. "On borders of swamps in

Fig. 2. Type material of *Chrysocoma virgata* Nuttall (BM, photograph at KSC).

New Jersey, near the sea-coast," *T. Nuttall* (apparent type material PH!, BM, photograph at KSC; see discussion following citation of type of 1. *Bigelowia nuttallii*). — *Bigelowia nudata* var. *virgata* (Nutt.) T. & G., Fl. N. Am. 2: 232. 1842. — *B. nudata* f. *virgata* (Nutt.) Gray, Proc. Am. Acad. Arts

Sci. 8: 646. 1873. — *Chondrophora nudata* var. *virgata* (Nutt.) Britton, Mem. Torrey Bot. Club 5: 317. 1894. — *Chondrophora virgata* (Nutt.) Greene, Erythea 3: 91. 1895. (All these names have been mistakenly applied to the preceding species, *B. nuttallii* L. C. Anderson.)

Cespitose herbs with short, thick caudices; stems (3.7) 5—7 (8) dm tall, often nearly scapose with reduced leaves; basal leaves oblanceolate, gradually attenuated into the short petiole, (4) 6.5—10.0 (14) cm long, (4) 6—9 (14) mm wide; cauline leaves (6) 10—13 (15), oblanceolate or spatulate, lowest ones (3) 4.5—6.0 (9) cm long, (2.5) 3.5—7.0 (12) mm wide; heads loosely clustered in rounded or flat-topped corymbose inflorescences; involucres 4.5—6.0 mm high with 10—17 bracts; flowers 2—5, 3.0—4.2 mm long, lobes 1.0—1.5 mm long; stigmatic lines noticeably longer than stigmatic appendages; achenes 1.2—1.6 mm long; pappus 2.8 mm long (Fig. 1, open circles).

Range: Moist sandy loams of savannahs, pine barrens, and margins of swamps in the coastal plain from North Carolina to Florida and westward to eastern Louisiana. Aug.-Nov.

Representative specimens: see Table 2.

2b. BIGELOWIA NUDATA (Michx.) DC. subsp. **australis** L. C. Anderson, subsp. nov.

Subrhizomatosa, caudices angusti; folia basalia saepe ultra 10 cm longa, infra 4 mm lata; corollae 4—5 mm longae; capitula 6.0—7.5 mm alta.

Somewhat rhizomatous, caudices narrow, 2.5—3.5 cm long; stems (2.2) 4—5 (8.6) dm tall; basal leaves linear oblanceolate to narrowly spatulate, (6) 9—14 (22) cm long, 2.0—4.5 mm wide; cauline leaves (5) 9—12 (19), lowest ones linear spatulate, (4.5) 7—10 (17) cm long, 1.5—3.0 mm wide; heads congested into somewhat rounded or flat-topped corymbose inflorescences; involucres 6.0—7.6 mm high, with 13—20 bracts; flowers 3—6 per head; corollas 4—5 mm long, lobes 1.4—1.8 mm long; stigmatic lines two-thirds the total style branch length; achenes 1.6—2.0 mm long; pappus 3.0—3.3 mm long (Fig. 1, closed circles).

Type: In pinelands, vicinity of Ft. Myers, Lee Co., Florida, 20 March 1916, *Jeanette P. Standley 28* (GH! MO! NY-holotype! US!).

Range: Rich sandy soil of wet prairies and open pinelands of peninsular Florida; its range rapidly being reduced by "advances of civilization" (Lakela, personal communication). This taxon occurs in areas usually free of killing frosts; consequently, blooming frequently occurs in the spring as well as during the autumn and winter months. Oct.-May.

Representative specimens: see Table 2.

Intergradation between the subspecies of *B. nudata* is limited (encircled dots, Fig. 1), possibly due to phenological variance. Some vegetative collections from northern Florida appear intermediate: Bradford Co.: near U.S. 301, *Radford 8248* (NCU); Flagler Co.: 5 mi E Seville, *Smith & Myint 451* (FSU); Union Co.: Danville, *Murrill 773* (US). A collection in flower, *Nash 2597* (GH, MO, NY, US) from Baldwin, Duval Co., shows intermediacy in several features. Involucral bract number and flower number suggest *B. n.*

TABLE 4. RANK CORRELATION OF SELECTED FLORAL FEATURES WITH GEOGRAPHIC DISTRIBUTION OF BIGELOWIA TAXA.

	B. nuttallii (D.F.=15)		*B. n. nudata* (D.F.=27)		*B. n. australis* (D.F.=11)	
Bract number						
Correlation coefficient	.776		.340		.552	
Significance		1%		—		10%
Involucral length						
Correlation coefficient	.727		.239		-.279	
Significance		1%		—		—
Involucral width						
Correlation coefficient	.874		-.257		.455	
Significance		1%		—		—
Flower number						
Correlation coefficient	.648		-.313		.185	
Significance		1%		—		—
Flower length						
Correlation coefficient	.521		-.102		.154	
Significance		5%		—		—

nudata, and length of involucre and flowers are more like *B. n. australis;* whereas the stigmatic line ratio is like that found in *B. nuttallii.*

The morphology of *B. n. australis* is intermediate to that of *B. n. nudata* and *B. nuttallii* in many respects (see Table 2). The phenotypic closeness to *B. nuttallii* may reflect derivation, in part, from ancient *nuttallii* stock; however, the features of largeness in *B. n. australis* morphology may be due simply to excellent adaptation of this taxon to the longer growing season.

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