A Revised Classification of *Antennaria* (Asteraceae: Inuleae) of the Eastern United States

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ABSTRACT. Review of morphology, cytology, breeding behavior, and field observations has resulted in a revised classification of *Antennaria* as represented in the eastern United States. Four sexual diploid ($n = 14$) species are recognized, namely *A. plantaginifolia, A. neglecta, A. solitaria,* and *A. virginica.* These diploids act as pillars that support a polyploid complex consisting of *A. Parlinii* s.l. with two subspecies including **A. Parlinii** subsp. **fallax**, comb. nov., and *A. neodioica* s.l. with three subspecies, including **A. neodioica** subsp. **canadensis**, comb. nov., and **A. neodioica** subsp. **petaloidea**, comb. nov. Many of the polyploids are apomictic and that has affected taxonomic difficulties.

Antennaria is a genus of dioecious, perennial, entire-leaved herbs that are distributed in temperate to arctic regions throughout the northern hemisphere with three species in the southern Andes of South America. The genus probably contains 20 to 30 sexual diploid species as well as many heteroploid agamic complexes derived from them. *Antennaria* was split off as a separate genus from *Gnaphalium* L. by Gaertner (1791). Taxonomic problems in the genus began to be identified in the late 1890s when botanists, namely Greene, E. Nelson, Fernald, and Rydberg, began discovering and naming variant populations as species. Apomixis in the genus has led to the formation of many distinct polyploid races or clones, many of which were named as species by these and other workers. A survey of the Gray Herbarium Card Index revealed that over 300 names have been proposed for North American *Antennaria* since 1897. Many were based on single collections from local populations that have probably never been recollected. Two opposing views are prevalent as to how *Antennaria* of the eastern United States should be classified. Fernald (1945, 1950) recognized the following 14 species from the eastern United States: *A. Brainerdii, A. campestris, A. canadensis, A. fallax, A. Farwellii, A. munda, A. neglecta, A. neodioica, A. Parlinii, A. petaloidea, A. plantaginifolia, A. rupicola, A. solitaria,* and *A. virginica.*

By contrast, Cronquist (1945, 1952) recognized "three fairly well marked species" including the small-leaved *A. neglecta,* the large-leaved, polycephalous *A. plantaginifolia,* and the large-leaved, monocephalous *A. solitaria.* A survey of floras published after 1945 has revealed that opinion

is divided as to which treatment to use. Correll and Johnston (Texas, 1970), Lakela (Minnesota, 1965), and Scoggan (Canada, 1979) continue to use a Fernald-like classification, whereas Steyermark (Missouri, 1963), Weishaupt (Ohio, 1971), and Barkley (Kansas, 1968) have used the Cronquist treatment. Recently Strausbaugh and Core (West Virginia, 1978) have used a hybrid Fernald-Cronquist classification. Beals (1968) and Beals and Peters (1966) in dealing with the species of Wisconsin, point out that because of the numerous apomicts of hybrid origin, intergradation with respect to morphological characteristics exists between all of the species. This is true even for those having broad (i.e., *A. Parlinii*) and those having narrow (i.e., *A. neodioica*) leaves. Beals (1968) adopted Fernald's classification but stated that treatments recognizing fewer species would also be acceptable. The purpose of this report is to provide a new classification for *Antennaria* based on morphology, chromosome numbers, cross compatibility, and numerous field observations.

Apomixis, polyploidy, and hybridization are all important factors in the evolution of the agamic complexes in *Antennaria* and are responsible for the formation of many microspecies, thus traditional taxonomic methods cannot be employed. The objective of this study was to produce a new classification of *Antennaria* in the eastern United States using the method advocated by Babcock and Stebbins (1938). The classification will be derived not only from morphology, as previous ones were, but also from breeding studies and chromosome numbers.

Materials and Methods

Field observations were made and over 200 clones representing a wide range of variation in *Antennaria* were cultivated in the greenhouse. Chromosome numbers were obtained from these plants and are reported elsewhere (Bayer and Stebbins 1981). Interspecific and interpopulational crosses were made in the greenhouse during the spring seasons of 1979–1980. To avoid other than intentional pollinations, immature capitula were covered with small paper bags (Kim-wipes) and tied at the bottom with string. Products of these crosses were later harvested to determine the percent seed set by examining the florets in a single capitulum. On the average five or six inflorescences per cross were scored to obtain an average seed set. Some capitula isolated in the greenhouse were left unpollinated to determine if any seed was set via agamospermy. Specimens were borrowed from CAN, CM, GH, MO, NDG, NY, OS, PAC, SDU, US, VPI, and WVA for morphological studies.

Results and Discussion

With respect to *Antennaria* in the eastern United States, there are four distinct, sexual diploid ($2n = 28$, Bayer and Stebbins 1981) species, these being *A. plantaginifolia, A. neglecta, A. solitaria,* and *A. virginica.* Results

of crossing experiments demonstrate that the sexual diploids set no seed when isolated, however, seed set ranges from 81–96% (table 1) when different populations of the same species are crossed. Sex ratios in these species are usually close to 1:1.

Antennaria plantaginifolia, a species with basal leaves having 3–7 principal veins, differs from its close diploid relative *A. solitaria* in that it has polycephalous inflorescences. When crossed the resulting seed set is an average of 63% indicating the close relationship of the two (table 1).

The other two diploid species, *A. virginica* and *A. neglecta,* are similar in that they both have small leaves with a single primary vein (fig. 1). They differ in that the leaves of *A. virginica* are distinctly petiolate while those of *A. neglecta* are non-petiolate (fig. 1). In addition, *A. neglecta* has a distinct flag-like appendage on its upper cauline leaves while *A. virginica* lacks the flag. Although *A. virginica* was treated as a variety of *A. neglecta* by Cronquist (1945, 1952), it is highly cross incompatible with *A. neglecta* (seed set is 10%, table 1) or with any of the other diploids and we suggest *A. virginica* to be a good biological species. The habitat of *A. virginica* is mesic shale barrens, primarily in West Virginia and Pennsylvania (fig. 4). By contrast, *A. neglecta* is widely distributed from Quebec west to the Northwest Territory, south to Colorado, and east to Virginia; it inhabits prairies and grazed pastures throughout its range (fig. 5). Taking into account the morphological and habitat differences along with the cross incompatibility, we feel that *A. neglecta* and *A. virginica* should be recognized as separate species.

Antennaria neglecta, which is morphologically distinct from *A. solitaria,* has a relatively high cross compatibility with *A. solitaria* (63% and 84% seed set, table 1). However, these two species are ecologically isolated, *A. neglecta* preferring dry, open habitats whereas *A. solitaria* occurs in mesic woodlands. Although *A. plantaginifolia* occasionally grows sympatrically with *A. virginica* and *A. neglecta,* it appears to be quite cross incompatible with them (5% and 6% seed set, table 1) when *A. plantaginifolia* is the pistillate parent. If *A. neglecta* is used as the pistillate parent and is crossed with *A. plantaginifolia* the cross compatibility is somewhat greater (41%). Putative hybrids between *A. virginica* and *A. plantaginifolia,* and between *A. virginica* and *A. neglecta,* have recently been found in West Virginia, where the taxa occasionally grow sympatrically. Some of these hybrids morphologically resemble polyploid agamospecies such as *A. canadensis* and *A. neodioica* and may offer some insight into the origin of these species.

Fertility and meiotic behavior of the F_1's have not been examined yet because these perennials grow slowly. Morphological measurements in the diploids agree with those given by Fernald (1950). The distributions of the diploids are shown in figures 2–5.

Two distinct polyploid groups occur in the eastern United States, those with 1-nerved basal leaves (*A. neodioica* s.l.) and those with large, 3–7-nerved leaves (*A. Parlinii* s.l.).

TABLE 1. Crossing data indicating staminate and pistillate parent *Antennaria* species (all diploid but *A. Parlinii*, which is hexaploid), their geographic origin, and the average resulting seed set. Vouchers (numbers in parentheses) are deposited at OS. In each case the voucher number refers to several plants of each gender collected at these localities. All crosses were made under controlled conditions in the greenhouse.

Pistillate parent	Geographic origin	Staminate parent	Geographic origin	Average number of seed set/florets per head	Average % seed set
A. solitaria (BC-22)	Adams Co., OH	*A. virginica* (BR-109)	Pendleton Co., WV	81/185	44
A. solitaria (BC-22)	Adams Co., OH	*A. neglecta* (BPN-56)	Delaware Co., OH	101/160	63
A. solitaria (BC-22)	Adams Co., OH	*A. plantaginifolia* (WSB-42)	Meade Co., KY	128/158	81
A. plantaginifolia (SB-104)	Abbeville Co., SC	*A. solitaria* (BC-22)	Adams Co., OH	45/101	45
A. plantaginifolia (MC-43)	Meade Co., KY	*A. neglecta* (BPN-56)	Delaware Co., OH	6/113	5
A. plantaginifolia (SB-104)	Abbeville Co., SC	*A. virginica* (BR-109)	Pendleton Co., WV	7/120	6
A. plantaginifolia (WB-46)	Whitley Co., KY	*A. Parlinii* ssp. *fallax* (OK-97)	Creek Co., OK	1/105	1
A. neglecta (BPN-56)	Delaware Co., OH	*A. solitaria* (BC-22)	Adams Co., OH	82/98	84
A. neglecta (BPN-56)	Delaware Co., OH	*A. virginica* (BR-109)	Pendleton Co., WV	9/86	10
A. neglecta (BPN-56)	Delaware Co., OH	*A. plantaginifolia* (WB-46)	Whitley Co., KY	38/92	41
A. Parlinii ssp. *fallax* (DA-1)	Franklin Co., OH	*A. plantaginifolia* (WB-46)	Whitley Co., KY	4/121	3
A. plantaginifolia (SB-104)	Abbeville Co., SC	*A. plantaginifolia* (CO-102)	Etowah Co., AL	126/130	97
A. virginica (AV-78)	Columbiana Co., OH	*A. virginica* (BR-109)	Pendleton Co., WV	86/93	92
A. neglecta (BPN-56)	Delaware Co., OH	*A. neglecta* (CR-82)	Fairfield Co., OH	106/110	96
A. solitaria (BC-22)	Adams Co., OH	*A. solitaria* (QS-101)	Polk Co., TN	132/163	81
A. Parlinii ssp. *Parlinii* (KX-18)	Knox Co., OH	*A. Parlinii* ssp. *fallax* (OK-93)	Payne Co., OK	127/146	87

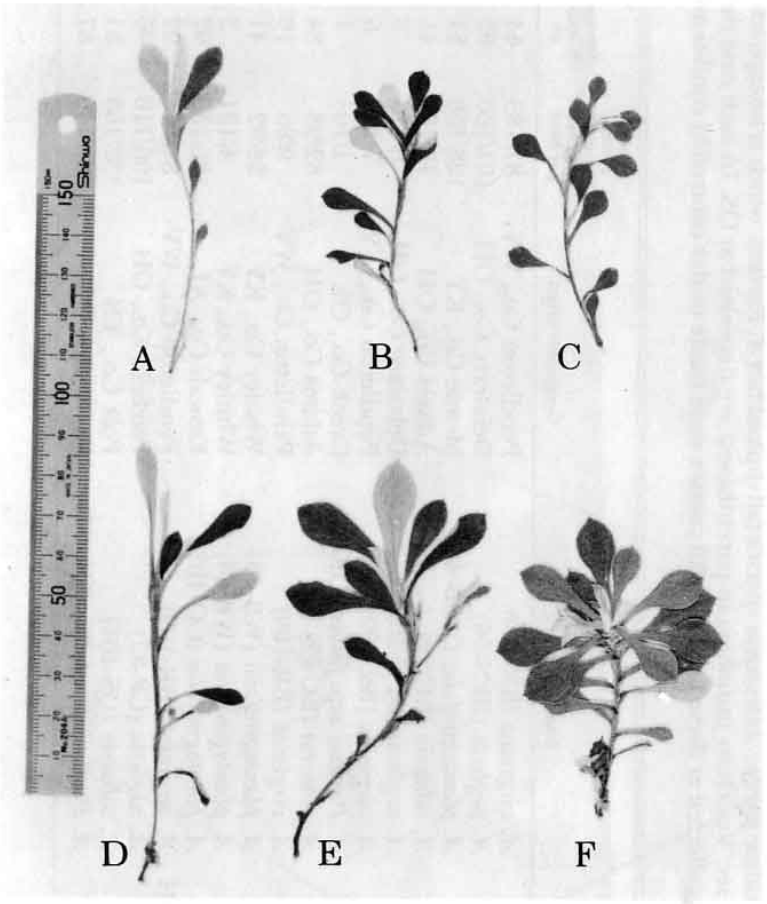
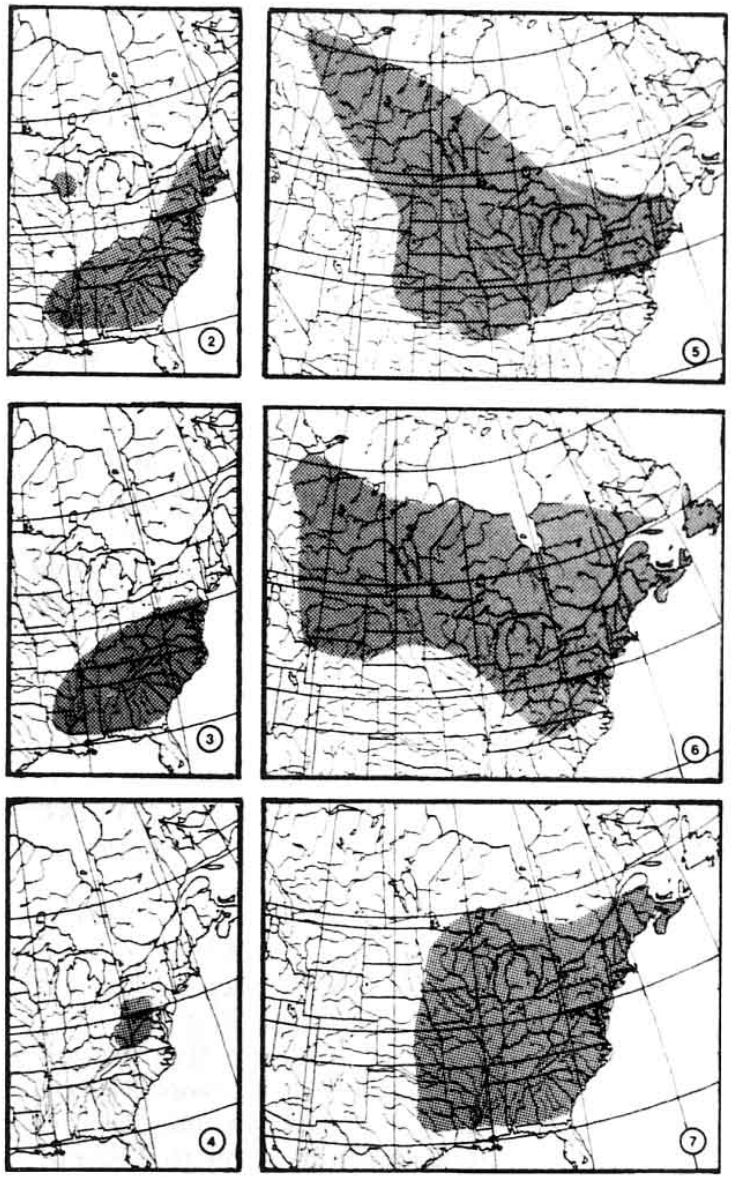


FIG. 1. Stolons of small-leaved species of *Antennaria* from plants grown in the greenhouse under uniform conditions. A. *A. neglecta* ($2n = 28$). B. *A. virginica* ($2n = 28$). C. *A. virginica* ($2n = 56$). D. *A. neodioica* subsp. *canadensis* ($2n = 56$). E. *A. neodioica* subsp. *petaloidea* ($2n = 84$). F. *A. neodioica* subsp. *neodioica* ($2n = 56$).

Polyploid *A. neodioica* s.l., in which we include *A. neodioica* s.str., *A. canadensis,* and *A. petaloidea,* consists of tetraploids and hexaploids ($2n = 56$ and 84; Bayer and Stebbins 1981). *Antennaria neodioica* s.l. has some characteristics of three of the eastern diploids, namely *A. neglecta, A. plantaginifolia,* and *A. virginica.* Stolons from the small-leaved diploids and polyploids are illustrated in figure 1, where it may be seen that *A. petaloidea* (fig. 1E) and *A. canadensis* (fig. 1D) have stolons more like *A. neglecta* (fig. 1A) in that the leaves on the basal part are reduced in size and number. *Antennaria neodioica* s.str. (fig. 1F) more closely resembles diploid *A. virginica* (fig. 1B) with respect to its stolons because it has leaves at the base of the stolons that are not as much reduced in size and number as those of *A. neglecta.* In fact, *A. neodioica* s.str. was once thought to be the autotetraploid (nonhybrid) derivative of *A. virginica* (Stebbins



FIGS. 2–7. Distributions of *Antennaria* species of the eastern United States. 2. *A. plantaginifolia*. 3. *A. solitaria*. 4. *A. virginica*. 5. *A. neglecta*. 6. *A. neodioica* s.l. 7. *A. Parlinii* s.l.

1935). A tetraploid individual of *A. virginica* (fig. 1C) that was recently found in West Virginia growing among diploid clones (fig. 1B) is morphologically similar to the diploids yet distinct from typical tetraploid *A. neodioica* s.str. (fig. 1F). *Antennaria neodioica* s.str. (fig. 1F) differs from *A. virginica* (fig. 1B, C) not only in its larger leaf size but in the length of its corolla (see key) and height of its involucre. The glabrous, bright green leaves of *A. canadensis* are found in none of the diploids. As discussed

earlier, it is plausible that the small-leaved apomicts are of hybrid origin. In *A. neodioica* s.l. male clones are extremely rare or absent in most cases and the species consists of obligate apomicts (Stebbins 1932). It seems best therefore to recognize all these small-leaved apomicts as one variable species, *A. neodioica,* with three reasonably distinct subspecies, *A. neodioica* subsp. *neodioica* (including *A. neodioica* s.str.), *A. neodioica* subsp. *canadensis* (including *A. canadensis*), and *A. neodioica* subsp. *petaloidea* (including *A. petaloidea* s.str.). For key characters separating the subspecies of *A. neodioica* s.l. refer to the key. The distribution of *A. neodioica* s.l. is given in figure 6.

Antennaria gaspensis Fern., which is confined mainly to Quebec and Newfoundland, is not considered in our treatment for the eastern United States. Cronquist (1952) called this agamospecies *A. neglecta* var. *gaspensis* and is of the opinion that it extends into northern Maine. After examining specimens, kindly sent by Prof. Cronquist from New York, it seems advisable to consider these four specimens from the Mattawamskeag River, Maine (topotypes of *A. rupicola* Fern. collected and identified by M. L. Fernald), as stunted variants of *A. rupicola* of Fernald (1950). "True" *A. rupicola,* included in this treatment as a synonym under *A. neodioica* subsp. *neodioica,* has subulate-tipped cauline leaves, yellow or straw-colored phyllaries, and greenish-gray, slightly pubescent basal leaves, as do the specimens sent by Cronquist. By contrast, *A. gaspensis,* has scarious-tipped appendages at tips of the cauline leaves, umber-colored phyllaries, and small, gray, heavily pubescent basal leaves. Thus on these features we assign these specimens to *A. rupicola* (=*A. neodioica* subsp. *neodioica*).

The large-leaved polyploids *A. Parlinii* s.l., in which we include *A. fallax, A. calophylla, A. munda, A. occidentalis,* and others, have some characteristics of diploid *A. plantaginifolia.* Nevertheless, the glabrous leaves found in typical *A. Parlinii* s.str. are not found in gray-green, tomentose-leaved *A. plantaginifolia.* This situation indicates that introgression from another glabrous-leaved diploid, possibly *A. racemosa* Richards. in Hook. of the western United States and/or *A. solitaria,* may be involved in the parentage of the polyploids. Recent results show that when glabrous *A. Parlinii* s.str. is crossed with pubescent *A. fallax,* the F_1 is intermediate with respect to pubescence (Bayer unpubl.). It is probable that in *A. Parlinii* s.l. this character is segregating. The chromosome numbers of *A. Parlinii* s.l. range from tetraploid to pentaploid, hexaploid, and octoploid ($2n$ = 56, 70, 84, and 112), with hexaploids being by far the most prevalent (Bayer and Stebbins 1981). When diploid *A. plantaginifolia* is crossed with sexual hexaploid *A. Parlinii* s.l. less than 3% seed is set (table 1). *Antennaria Parlinii* s.l. differs from *A. neodioica* s.l. in that in the former sexual populations are common (apomictic ones are also found) whereas in the latter apomictic populations are widespread (sexual ones are unknown). Thus, because *A. Parlinii* s.l. is probably of hybrid (allopolyploid) origin and is genetically isolated from the diploids, it seems

best to recognize two reasonably distinct subspecies: *A. Parlinii* subsp. *Parlinii* (including *A. arnoglossa*) and *A. Parlinii* subsp. *fallax* (including *A. calophylla* s.str. and *A. munda* s.str.). Subspecies *fallax* differs from subspecies *Parlinii* in that the former has pubescent adaxial leaf surfaces while in the latter they are glabrous. The range of *A. Parlinii* s.l. is illustrated in figure 7.

Two methods of classification had previously been used, the first of these being to give each apomictic form a specific epithet. This procedure is unsatisfactory in most instances because it leads to an enormous number of species that are usually not separated clearly from one another. This procedure has been used by European workers with *Taraxacum* and *Hieracium*. The second method classifies entire complexes as single species that, as Babcock and Stebbins (1938) put it, "would be enormous, unwieldy taxonomic units, of no practical value." Such a classification has been used to some extent by Cronquist (1945) in which all small-leaved *Antennaria* in the northeastern United States were called *A. neglecta*.

The method of classification used by Babcock and Stebbins (1938) first delimits the sexual diploid species in the complexes and gives them each a specific epithet. These species then act as pillars that support the polyploid sexual and agamic complexes. Autopolyploid (nonhybrid) microspecies that cannot be easily distinguished from their sexual diploid progenitors are included taxonomically with the sexual diploid.

Apomicts of many genera are of hybrid origin (allopolyploids), therefore it is difficult to assign them to a sexual diploid species because they combine morphological characteristics of their parents (Gustafsson 1946–1947). Babcock and Stebbins (1938) suggested, however, that these polyploid sexual and agamospecies could be clustered into a single species that may be separated further into subspecies and forms.

The classification presented in this paper differs from that of Babcock and Stebbins (1938) in that it groups the apomicts with the sexual allopolyploids instead of grouping the allopolyploids with one of the sexual diploids. Furthermore the agamic polyploids are grouped as species with their own distinct specific epithets.

KEY TO *ANTENNARIA* OF THE EASTERN UNITED STATES

Heads solitary ..... *A. solitaria*
Heads two or more per inflorescence.
  Basal leaves prominently 3–7-nerved.
    Pistillate involucres 5–7 mm high; pistillate corollas 3–4 mm high; staminate corollas 2–3.5 mm high; basal leaves tomentose adaxially; young stolons mostly ascending; staminate and pistillate plants equally common; plants of Appalachians, Piedmont, the Atlantic seaboard, and the driftless area of Wisconsin and Minnesota ..... *A. plantaginifolia*
    Pistillate involucres 7–10 mm high; pistillate corollas 4–7 mm high; staminate corollas 3.5–5 mm high; basal leaves tomentose or glabrous adaxially; young stolons mostly decumbent; sexual and apomictic populations present; plants widespread throughout the eastern United States.

Basal leaves glabrous adaxially or nearly so; summit of young cauline stem usually glandular ..... *A. Parlinii* subsp. *Parlinii*
Basal leaves tomentose adaxially; summit of young cauline stem usually glandless ..... *A. Parlinii* subsp. *fallax*
Basal leaves prominently 1-nerved.
Stolons 8–12 cm long, procumbent, leaves along the stolon smaller than those of the basal rosette; basal leaves gradually tapering to the base, non-petiolate.
Young leaves glabrous above, bright green; pistillate plants common, staminate rare or absent; widespread above terminal glacial margin .... *A. neodioica* subsp. *canadensis*
Young leaves tomentose adaxially, gray-green; staminate plants equal in number to pistillate or completely absent.
Upper cauline leaves tipped by a flat or curled scarious, flag-like tip; involucral bracts brown at base; pistillate and staminate plants equally common ..... *A. neglecta*
Upper cauline leaves subulate or only those about the corymb scarious-tipped; involucral bracts white or green at base; pistillate plants common, staminate absent ..... *A. neodioica* subsp. *petaloidea*
Stolons 5–8 cm long, decumbent, leaves along the stolon about equal in size to those of the basal rosette; basal leaves having a distinct petiole or nearly so.
Pistillate involucres 4.5–7 mm high; pistillate corollas 3.2–4.5 mm long; plants of shale barrens of West Virginia, Virginia, Maryland, Pennsylvania, and locally in Ohio; staminate and pistillate plants common ... . *A. virginica*
Pistillate involucres 7–9 mm high; pistillate corollas 3.2–6 mm long; plants widespread; above glacial margin in the eastern United States; pistillate plants common, staminate rare or absent ..... *A. neodioica* subsp. *neodioica*

Accepted Taxa and Synonymy

1. Antennaria neglecta Greene, Pittonia 3:173. 1897.—Lectotype (here designated): USA, District of Columbia, Catholic University grounds, 3 May 1897, *E. L. Greene s.n.* (NDG!).

Antennaria campestris Rydb., Bull. Torrey Bot. Club 24:304. 1897.—Type: USA, Nebraska, Lincoln, Jun 1887, *Webber s.n.* (syntype: NY!).

Antennaria Wilsonii Greene, Amer. Midl. Naturalist 2:78. 1911.—Lectotype (here designated): USA, Indiana, Hamilton Co., near Cold Creek, 18 Apr 1892, *G. Wilson s.n.* (US!).

Antennaria erosa Greene, Amer. Midl. Naturalist 2:79. 1911.—Lectotype (here designated): USA, Illinois, Odin, "Part of original", 8 May 1909, *E. L. Greene s.n.* (NDG!).

Antennaria longifolia Greene, Amer. Midl. Naturalist 2:79. 1911.—Lectotype (here designated): USA, Missouri, Grain Valley, common on prairie, 7 May 1899, *B. F. Bush 6* (US!).

Antennaria parvula Greene, Amer. Midl. Naturalist 2:81. 1911.—Lecto-

TYPE (here designated: USA, South Dakota, Black Hills, near Ft. Meade, 1887, *W. H. Forwood s.n.* (US!).

Antennaria Lunellii Greene, Amer. Midl. Naturalist 2:81. 1911.—LECTOTYPE (here designated): USA, North Dakota, Benson Co., Leeds, 7 May 1902, *J. Lunell s.n.* (US!).

Antennaria chelonica Lunell, Amer. Midl. Naturalist 2:126. 1911.—LECTOTYPE (here designated): USA, North Dakota, Turtle Mountains, Rolette Co., near St. John, 6 Jun 1911, *J. Lunell s.n.* (IND!).

2. **Antennaria neodioica** Greene subsp. **canadensis** (Greene) Bayer & Stebbins comb. et stat. nov.—*Antennaria canadensis* Greene, Pittonia 3:275. 1898.—LECTOTYPE (here designated): Canada, New Brunswick, rocky places, Campbellton, 8 Jul 1876, *R. Chalmers, Canadian survey # 11299* (CAN!).

Antennaria canadensis Greene var. *Randii* Fern., Proc. Boston Soc. Nat. Hist. 28:246. 1898.—*Antennaria neglecta* Greene var. *Randii* (Fern.) Cronq., Rhodora 47:184. 1945.—LECTOTYPE (here designated): USA, Maine, Mt. Desert Island, near Indian Pond, 1 Jul 1897, *Rand s.n.* (GH!).

Antennaria canadensis Greene var. *spathulata* Fern., Rhodora 16:132. 1914.—*Antennaria spathulata* (Fern.) Fern., Rhodora 16:196. 1914.—TYPE: Canada, Newfoundland, Valley of Exploits River and Point Riche, Aug 1910 and 1911, *M. L. Fernald and K. M. Wiegand 6362 and 4143* (syntypes: GH!).

3. ANTENNARIA NEODIOICA Greene subsp. NEODIOICA, Pittonia 3:184. 1897.—LECTOTYPE (here designated): USA, Pennsylvania, Bus[h]-kill, 1 Jun 1897, *E. L. Greene s.n.* (NDG!).

Antennaria neodioica Greene var. *attenuata* Fern., Proc. Boston Soc. Nat. Hist. 28:245. 1898.—*Antennaria neglecta* Greene var. *attenuata* (Fern.) Cronq., Rhodora 47:184. 1945.—LECTOTYPE (here designated): USA, Connecticut, New Haven, wooded hillsides, 17 May 1898, *Evans and M. L. Fernald s.n.* (GH!).

Antennaria neodioica Greene var. *grandis* Fern., Rhodora 1:73. 1899.—LECTOTYPE (here designated): USA, Maine, roadside, Town Hill Road, Somesville, 1 Jul 1897, *Rand s.n.* (GH!).

Antennaria rupicola Fern., Rhodora 1:74. 1899.—TYPE: USA, Maine, Aroostook Co., ledgy shore and rocky banks, Island Falls, 9 Jun 1898, *M. L. Fernald 2361* (GH!).

Antennaria neodioica Greene var. *chlorophylla* Fern., Rhodora 23:296. 1922.—TYPE: USA, Maine, Penobscot Co., lower Penobscot Valley, gravelly bank, Orono, 4 Jun 1898, *M. L. Fernald s.n.* (GH!).

Antennaria neodioica Greene var. *typica* Fern., Rhodora 35:345. 1933.—LECTOTYPE (here designated): Canada, Newfoundland, Grand Falls, gravelly terrace north bank of river below falls, 4 Jul 1911, *M. L. Fernald and K. M. Wiegand 6360* (GH!).

Antennaria neodioica Greene var. *interjecta* Fern., Rhodora 35:345. 1933.—TYPE: Canada, Quebec, Rimouski Co., dry fir woods at base of limestone conglomerate cliffs, peak west of Baptiste Michoud's, Bic, 16 Jul 1904, *Collins and M. L. Fernald s.n.* (GH!).

4. **Antennaria neodioica** Greene subsp. **petaloidea** (Fern.) Bayer & Stebbins comb. et stat. nov.—*Antennaria neodioica* var. *petaloidea* Fern., Proc. Boston Soc. Nat. Hist. 28:245. 1898.—*Antennaria petaloidea* (Fern.) Fern., Rhodora 1:73. 1899.—LECTOTYPE (here designated): USA, New Hampshire, near town hall, Jaffrey, 31 May 1897, *Rand and Robinson 428* (GH!).

Antennaria neglecta Greene var. *subcorymbosa* Fern., Proc. Boston Soc. Nat. Hist. 28:246. 1898.—*Antennaria petaloidea* (Fern.) Fern. var. *subcorymbosa* (Fern.) Fern., Rhodora 16:133. 1914.—LECTOTYPE (here designated): USA, Maine, Mt. Desert Island, Seal Harbor, roadside, "Davis Farm", 9 Jul 1897, *E. L. Rand s.n.* (GH!; isolectotypes: GH!).

Antennaria petaloidea (Fern.) Fern. var. *scariosa* Fern., Rhodora 1:73. 1899.—LECTOTYPE (here designated): USA, Maine, Penobscot Co., lower Penobscot Valley, abundant on sandy, open hillsides, Orono, 3 Jun 1898, *M. L. Fernald 2395* (GH!; isolectotype: CAN!).

Antennaria appendiculata Fern., Rhodora 23:295. 1922.—TYPE: Canada, Quebec, Gaspé Co., banks of the Grand River, dry wooded knolls, 30 Jun–3 Jul 1904, *M. L. Fernald s.n.* (GH!; isotypes: CAN!, GH!).

Antennaria petaloidea (Fern.) Fern. var. *novaboracensis* Fern., Rhodora 23:296. 1922.—TYPE: USA, New York, Tompkins Co., dry fields near Key Hill Swamp, Newfield, 21 May 1919, *A. E. Eames and K. M. Wiegand 13073* (GH!).

5. **Antennaria Parlinii** Fern. subsp. **fallax** (Greene) Bayer & Stebbins comb. et stat. nov.—*Antennaria fallax* Greene, Pittonia 3:321. 1898.—LECTOTYPE (here designated): USA, District of Columbia, Terra Cotta, 23 Apr 1898, *E. L. Greene s.n.* (NDG!).

Antennaria arnoglossa Greene var. *ambigens* Greene, Pittonia 3:320. 1898.—*Antennaria Parlinii* Fern. var. *ambigens* (Greene) Fern., Proc. Boston Soc. Nat. Hist. 28:243. 1898.—*Antennaria ambigens* (Greene) Fern., Rhodora 1:150. 1899.—*Antennaria plantaginifolia* (L.) Richards. var. *ambigens* (Greene) Cronq., Rhodora 47:183. 1945.—The type of this name should be from Washington, D.C., (not found in NDG or US). Fernald (Proc. Boston Soc. Nat. Hist. 28:244. 1898.) evidently saw a specimen of E. L. Greene's from Washington, D.C., but the location of this specimen is unknown. Based on the original description and additional descriptions by Fernald (see above), as well as Cronquist (1945), this taxon is placed in synonymy under *Antennaria Parlinii* subsp. *fallax*.

Antennaria occidentalis Greene, Pittonia 3:320. 1898.—LECTOTYPE (here designated): USA, Illinois, near Oquawka, Jul 1874, *H. N. Patterson s.n* (NDG!).

Antennaria Farwellii Greene, Pittonia 3:347. 1898.—*Antennaria Parlinii* Fern. var. *Farwellii* (Greene) Boivin, Naturaliste Canad. 94:645. 1967.—TYPE: USA, Michigan, Keweenaw Co., 15 May 1884, *O. A. Farwell 78* (NDG!).

Antennaria calophylla Greene, Pittonia 3:347. 1898.—*Antennaria fallax* Greene var. *calophylla* (Greene) Fern., Rhodora 38:230. 1936.—LECTOTYPE (here designated): USA, Illinois, Cobden, 15 Jun 1898, *E. L. Greene s.n.* (NDG!; isolectotypes: NDG!).

Antennaria Brainerdii Fern., Rhodora 1:153. 1899.—LECTOTYPE (here designated): USA, Vermont, Ferrisburgh, low woods, 4 Jun 1899, *E. Brainerd 27* (GH!).

Antennaria mesochora Greene, Pittonia 5:111. 1903.—LECTOTYPE (here designated): USA, Michigan, Lake Goguac, 19 May 1902, *E. L. Greene s.n.* (NDG!).

Antennaria Greenei Bush, Annual Rep. Missouri Bot. Gard. 17:124. 1906.—LECTOTYPE (here designated): USA, Texas, Dallas, common in sandy woods, 1 Apr 1900, *J. Reverchon 330* (MO!).

Antennaria umbellata Greene, Amer. Midl. Naturalist 2:82. 1911.—LECTOTYPE (here designated): USA, Michigan, vicinity of Benton Harbor, on hillside, with violet[s], 27 May 1909, *E. L. Greene s.n.* (NDG!; isolectotypes: NDG!).

Antennaria Arkansana Greene, Leafl. Bot. Observ. Crit. 2:146. 1911.—LECTOTYPE (here designated): USA, Arkansas, Fulton, common in woods, 4 Apr 1900, *B. F. Bush 510* (US!).

Antennaria bifrons Greene, Leafl. Bot. Observ. Crit. 2:147. 1911.—LECTOTYPE (here designated): USA, Michigan, Port Huron, 9 Jun 1909, *E. L. Greene s.n.* (NDG!; isolectotype: NDG!).

Antennaria ampla Bush, Amer. Midl. Naturalist 3:352. 1914.—TYPE: USA, Missouri, high butte, 22 May 1914, *B. F. Bush 7119* (US!).

Antennaria munda Fern., Rhodora 38:229. 1936.—TYPE: USA, Maine, Penobscot Co., Orono, sandy wooded slope, 31 May 1901, *M. L. Fernald s.n.* (GH!).

6. ANTENNARIA PARLINII Fern. subsp. PARLINII, Gard. & Forest 10:284. 1897.—TYPE: USA, Maine, N. Berwick, 15 May 1891, *J. C. Parlin s.n.* (GH!).

Antennaria arnoglossa Greene, Pittonia 3:318. 1898.—*Antennaria Parlinii* Fern. var. *arnoglossa* (Greene) Fern., Proc. Boston Soc. Nat. Hist. 28:243. 1898.—*Antennaria plantaginifolia* (L.) Richards. var. *arnoglossa* (Greene) Cronq., Rhodora 47:183. 1945.—TYPE: USA, Virginia (not found in NDG; US). Greene's description of this species is very vague concerning designation of the type. Although he says "the species is Virginian" most of the specimens in his herbarium are from the District of Columbia. Any of a number of specimens of the correct age and labeled *Antennaria arnoglossa* in Greene's handwriting could serve as a neotype if the actual type is not found.

7. ANTENNARIA PLANTAGINIFOLIA (L.) Richards. in Hooker, Fl. Bor. Amer. 1:330. 1834.—*Gnaphalium plantaginifolium* L., Sp. Pl. 850. 1753.—TYPE: USA, *K[alm]*. (LINN, microfiche # 989.68!); see also B. L. Robinson. Rhodora 3: 11–13. 1901.

Antennaria decipiens Greene, Pittonia 3:278. 1898.—LECTOTYPE (here designated): USA, District of Columbia, Terra Cotta, 11 May 1898, *E. L. Greene s.n.* (NDG!).

Antennaria nemoralis Greene, Pittonia 4:41. 1899.—TYPE: USA, Tennessee, Knoxville, Apr 1898, *A. Ruth 624* (MO!).

Antennaria pinetorum Greene, Leafl. Bot. Observ. Crit. 2:147. 1911.—TYPE: USA, Virginia, Portsmouth, pine woods, 27 Apr 1898, *T. H. Kearney 1* (US!).

8. ANTENNARIA SOLITARIA Rydb., Bull. Torrey Bot. Club 24:304. 1897.—*Antennaria plantaginifolia* (L.) Richards. "β" *monocephala* Torr. & Gray, Fl. N. Amer. 2:431. 1843.—*Antennaria monocephala* (Torr. & Gray) Greene, Pittonia 3:176. 1896, not DC., Prodr. 6:269. 1837.—TYPE: USA, Louisiana, *Prof. Carpenter s.n.* (NY!). In raising *A. monocephala* to specific rank, Greene created a later homonym. Realizing this Rydberg created the epithet "solitaria" in 1897.

9. ANTENNARIA VIRGINICA Steb., Rhodora 37:230. 1935.—TYPE: USA, West Virginia, Hampshire Co., open woods, in shaly soil, Hanging Rock, 15 May 1933, *Frye 3* (GH!; isotypes: US).

Antennaria virginica Steb. var. *argillicola* Steb., Rhodora 37:232. 1935.—*Antennaria neodioica* Greene var. *argillicola* (Steb.) Fern., Rhodora 38:230. 1936.—*Antennaria neglecta* Greene var. *argillicola* (Steb.) Cronq., Rhodora 47:184. 1945.—TYPE: USA, West Virginia, Hampshire Co., open woods and roadsides, in shaly soil, Hanging Rock, May 1933, *Frye 1 and 10* (GH!; isotypes: US).

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