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A NEW SPECIES OF ANTENNARIA FROM THE APPALACHIAN REGION

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IN 1931, while studying the cytology of *Antennaria*, I noticed some specimens from Virginia identified as *A. neodioica* which looked smaller than the usual forms, and which appeared to be blooming earlier than typical *A. neodioica* in the same region. Some of these, moreover, had abundant staminate plants, which are notably rare, though occasionally found, in *A. neodioica*. Through the kindness of Mr. F. W. Hunnewell, one of whose collections was of this small form, I had an opportunity of examining the specimens in his personal collection, and found several sheets of it, some of which contained only staminate plants. One collection, from a large shale slope on Three Top Mt., Strasburg, Va., was very characteristic, and Mr. Hunnewell told me of its great abundance in that locality. Accordingly, I visited the spot in the spring of 1932, and although I was too early to obtain mature plants, I could recognize from the young buds that the staminate plants were as abundant as the pistillate, if not more so. I gathered enough young plants so that I could bring them to flower in pots, and found that they corresponded exactly with Mr. Hunnewell's specimens. The same spring I examined specimens in the herbarium of Dr. S. F. Blake, collected by Dr. H. A. Allard on a different part of the same hill. These were all staminate, and of the same size as the Hunnewell specimens, but differed considerably in the shape of the basal leaves and of the involucre bracts.

In the following year, 1933, Dr. Earl L. Core, of the University of West Virginia, very kindly met me at Hanging Rock, W. Va., and

took me to the farm of Wilbert M. Frye, about two and a half miles north of U. S. Highway no. 50, and lying in a narrow valley underlain by shale of Devonian age. We spent the day walking over the farm with Mr. Frye, and in the soft shaly soil, both along the roadside and in the open woods, the small *Antennaria* was very abundant, with the staminate plants again more common than the pistillate. Although the date was only April thirteenth, the plants were almost in bloom in sunny spots, and as far advanced as those of *A. plantaginifolia*. The few plants of *A. neglecta* seen had only tight buds among the basal leaves, while in typical *A. neodioica*, which was common, and easily distinguished by its larger, longer-petioled leaves, the plants were not far beyond their winter condition, and buds were not yet in evidence. In many places, the small plants were very conspicuous from the rosy pink bracts of the staminate involucre.

On my return from Hanging Rock, I found the same form at two places along route 50 in Virginia; west of Gore and east of Hayfield, although at the former locality it was too young to collect.

Later in the season, Mr. Frye very generously made a large collection for me of all the forms of *Antennaria* occurring around Hanging Rock, on the basis of which the differences between the small species and *A. neodioica* were quite apparent, and two different varieties of the former could be recognized. In their extreme forms they looked quite distinct, but they apparently intergrade so freely that they had best be described as well marked varieties of the same species.

More recently, I have re-examined specimens from the Gray Herbarium (cited as G.) through the kindness of Mr. Weatherby, and Mr. Hunnewell's collection, (cited as F. W. H.) and have examined others from the United States National Herbarium (U. S.), the herbaria of the Carnegie Museum at Pittsburgh (Pitt.) and of the Academy of Natural Sciences at Philadelphia (Phila.); from the personal collection of Dr. S. F. Blake (S. F. B.) and of my own collection, (G. L. S.) which includes specimens sent me by Miss Lena Artz, of Woodstock, Va. To all those whose kind generosity has made these specimens available I wish to express my thanks and appreciation.

Antennaria virginica, sp. nov., stolonibus foliosis 0.6–2.5 cm. longis; foliis basilaribus cuneato-oblanco-latis, acutis, mucronatis, petiolatis, cum petiolo 10–25 mm. longis, 3–7 mm. latis, tomentosis; caule florifero plantae masculae 3–12 cm. alto; foliis caulinis 4–7, tomentosis, linearibus, mediis 10–14 mm. longis, 0.5–1.8 mm. latis, superioribus 5–10 mm. longis apice scarioso lanceolato 0.5–2 mm. longo munitis; capitulis masculis 1–5, dense corymbosis, pedunculis 0.5–4 mm.

longis; involucrio masculino 3.8–5 mm. alto, bracteis biseriatis, anguste oblongis, obtusis vel acutis, margine erosis, lacteis vel stramineis; corolla 2.5–3.5 mm. longo; capillis pappi dilatatis, profunde dentatis vel acute lobatis; caule florifero plantae femineae 6–20 cm. alto; foliis caulinis 5–7, apice attenuatis, scariosis vel herbaceis; capitulis femineis 1–6, dense corymbosis; pedunculis 1–10(–25) mm. longis; involucrio femineo 4.5–6.5 mm. alto, bracteis 3–4-seriatis, oblongis vel lanceolatis, exterioribus obtusis vel acutis, 0.8–0.9 mm. latis, interioribus acuminatis, 0.5–0.6 mm. latis, margine erosis, lacteis vel stramineis; corolla 3.2–4.2, cum stylo 3.8–5 mm. longo, stylo exserto bifido, acheniis sparse pubescentibus, 1.1–1.3 mm. longis.—Very locally in Vermont and central New York (?), and from southern Pennsylvania through the Appalachian mountain region to Virginia and West Virginia. The following specimens have been examined. VERMONT: Middlebury, *E. Brainerd*, May 14 and 30, pist., in part (as *A. neodioica*, U. S.). PENNSYLVANIA: roadside bank, in dry shaly soil along Sherman's Creek, west of Dromgold, Perry County, *G. L. Stebbins Jr.*, no. 1050, stam. (G. L. S.). VIRGINIA: steep railroad embankment, in red, shaly soil, foot of Signal Knob, near Strasburg, Shenandoah County, *H. A. Allard*, May 16, 1931, stam., as *A. neodioica* (S. F. B.); same locality, *S. F. Blake*, no. 11735 stam. (S. F. B.); shale slopes, Woodstock, *Lena Artz*, April 30, 1933, in part, pist. (G. L. S.); low ground under pines, East Furnace, Shenandoah County, *Artz*, April 29, 1933; dry woods, Covington, Alleghany County, *F. W. Hunnewell*, no. 4096 stam. as *A. neodioica* (F. W. H.); dry woods, Hot Springs, Bath County, *F. W. Hunnewell*, no. 4097 in part, as *A. neodioica* stam. (in F. W. H.), pist. (in G.); Bedford County, *A. H. Curtiss*, 1871 stam. as *A. neodioica* (G., U. S.). WEST VIRGINIA: dry, open woods and roadsides, in shaly soil, Hanging Rock, Hampshire County, *Earl Core*, *W. M. Frye* and *G. L. Stebbins, Jr.*, no. 1031 stam. (G. L. S.); *W. M. Frye*, nos. 3 (TYPE, in Gray Herbarium, stam. and pist.), 4, 5, 6, 7, 11, stam. and pist. (G. L. S., G., U. S., S. F. B.); dry, open woods, White Sulphur Springs, Greenbrier County, *F. W. Hunnewell*, no. 2712 stam. as *A. neodioica* (F. W. H.).

Antennaria virginica can be distinguished from all varieties of *A. neodioica* by its slenderer stems, shorter, narrower cauline leaves, somewhat smaller involucries, shorter corollas, and by the scarious appendages on the upper cauline leaves of the staminate, and often the pistillate plants. In the latter characteristic, as well as in the shape of the basal leaves, it approaches *A. canadensis*, but differs from that species in the tomentose upper surface of the basal leaves, and in its much smaller involucries and corollas. In its floral characters, both as to size and morphology, *A. virginica* most nearly resembles *A. plantaginifolia*, but it is otherwise totally different, being of the small-leaved group. Typical *A. virginica*, moreover, is set off from all other species of the eastern United States by two charac-

teristics, the erose margins of the involucre bracts, and the sparsely pubescent achenes. It flowers about two weeks earlier than *A. neodioica*, and at the same time as *A. plantaginifolia*.

The typical form is apparently fairly common in dry woods in the Appalachian region of Virginia and West Virginia, wherever the underlying rock is shale, and occurs less commonly outside of the shale areas. The specimens from Vermont and New York are unexpected extensions of its range northward. The former is in every way characteristic of the pistillate plant, even possessing the scarious appendages on the cauline leaves. Although the staminate plant was apparently not collected, in view of its abundance southward, it should be looked for in the vicinity of Middlebury. A collection from New York, dry woods, altitude 2500 ft., Platte Clove, Catskill Mountains, C. S. Williamson, July 10, 1903 (Phila.) may be of this species. The basal leaves, inflorescences, involucres, corollas, and achenes are characteristic, but the cauline leaves are somewhat broader than in the southern material, and the upper ones, along with the upper part of the stems, are covered with red glandular hairs. In this case, also, the staminate plant was not collected.

The extreme of *A. virginica* which is most common on the open shale barrens may be described as

Var. **argillicola** n. var., a forma typica differt foliis basilaribus obovatis, 6–8 mm. latis, apice obtusis vel breviter mucronatis; foliis caulinis apice acutis vel breviter mucronatis, herbaceis; bracteis involucri masculi oblongis vel ellipticis, obtusis, margine integris, lacteis vel roseis; capillis pappi flosculi masculi dilatatis crenatis; involucre femineo 5.5–7 mm. alto; bracteis 0.4–0.8 mm. latis, exterioribus acutis, interioribus attenuatis, margine integris; achaeniis dense pubescentibus.—PENNSYLVANIA: dry, hilly woods, branch of Turkey Foot Run, Sewickley township, Allegheny County, *J. H. Schafer*, July, 1886 stam. (as *A. neodioica*, Pitt.); Moon township, Allegheny County, *Schafer*, no. 263 pist. (as *A. neodioica*, Pitt.). MARYLAND: Tonoloway Ridge, Washington County, *Shreve and Jones*, no. 768 pist. (as *A. neodioica*, U. S.). VIRGINIA: shale slope, along Gap Run, east of Hayfield, Frederick County, *G. L. Stebbins Jr.*, no. 1035 stam. (G. L. S.); shale slope, Three Top Mountain, Shenandoah County, *F. W. Hunnewell*, no. 11493, in part, stam and pist. (as *A. neodioica*, F. W. H.); same locality, *S. F. Blake*, nos. 11739 stam. and 11740 pist. (S. F. B.); Bull Pasture Mt., Shenandoah Mountains, *P. A. Rydberg*, no. 9004 stam. (as *A. neodioica*, U. S.); dry shale slope in mountains east of Natural Bridge, *E. B. Bartram*, May 31, 1909, pist. (as *A. neodioica*, Phila.). WEST VIRGINIA: dry woods and roadsides, in shaly soil, Hanging Rock, Hampshire County, *Earl Core*, *W. M. Frye*, and *G. L. Stebbins, Jr.*, no. 1033 stam. (G. L. S.); *W. M. Frye*, nos.

1, 2, 8, 10, stam. and pist. The latter number is the TYPE, in the Gray Herbarium, with a duplicate in the U. S. National Herbarium.

The material from Strasburg, Hanging Rock, and Hayfield is most characteristic, the other specimens show some transition toward the typical form.

In the breadth of its basal leaves, the absence of scarious appendages on the cauline leaves, the entire margins of the involucre bracts, and the densely pubescent achenes, var. *argillicola* resembles *A. neodioica*. Furthermore, the involucre of some pistillate plants equals in height that of typical *A. neodioica*. It may be recognized, however, by the short, narrow cauline leaves, and the narrow involucre bracts, as noted in the chart presented below, as well as its smaller size and more densely corymbose inflorescence. Its extreme form is also distinctive in the rounded basal leaves with very short mucros, and in the rose-colored involucre of the staminate plants. These do not occur regularly in any other of the species of eastern America, although they have been reported for *A. plantaginifolia*,¹ and seen by the writer in an immature plant, probably a form of *A. fallax*, collected in the shale area of Virginia.

This species and variety form an interesting addition to the plants of the Appalachian shale area, as studied by Wherry.² He has considered at least two of these, *Trifolium virginicum* and *Senecio antennariifolius*, relic species, descendants of ancestors which were widespread in pre-glacial time. *Antennaria virginica* must also be considered an old species compared to its more familiar relatives. As I have pointed out in a previous paper,³ the cytological evidence shows clearly that the parthenogenetic species of *Antennaria* have been derived from their nearest relatives among the sexual species. *A. virginica*, with its abundant staminate plants, must be sexually reproducing.⁴ *A. neodioica* is known to be parthenogenetic, and shows in its specific characteristics that it has been derived from *A. virginica*. It is larger in all of its parts, and blooms later, while staminate plants are rare. These are precisely the characteristics in which the parthenogenetic *A. fallax*, *A. occidentalis*, and *A. petaloidea* differ from the sexual *A. plantaginifolia* and *A. neglecta*. In the accompanying chart

¹ R. Peabody, RHODORA 36: 376. 1934.

² Jour. Wash. Acad. Sci. 20: 43-52. 1929; Proc. Penn. Acad. Sci. 7: 16-164. 1933.

³ G. L. Stebbins, Jr., Bot. Gaz. 94: 338-340. 1932.

⁴ Since this has gone to press, bagging experiments, like those described in a previous paper (l. c.) have been performed on *A. virginica*. These had negative results, although bagged, but artificially pollinated inflorescences from the same plants produced a good percentage of mature achenes. This demonstrates that *A. virginica* is sexually reproducing, and not regularly parthenogenetic.

and drawings, the chief characteristics of *A. virginica* and its var. *argillicola* are compared with those of *A. neodioica* and its var. *attenuata*, the two varieties which are common within the range of *A. virginica*.

	A. VIRGINICA var. TYPICA	A. VIRGINICA var. ARGILLI- COLA	A. NEODIOICA var. TYPICA	A. NEODIOICA var. ATTENU- ATA
BASAL LEAVES				
Length	average 18-23 mm.	average 15-20 mm.	average 27-33 mm.	average 24-30 mm.
Breadth	av. 4-6 mm.	av. 6-8 mm.	av. 8-9 mm.	av. 9-10 mm.
Apex	acute mucro over 0.5 mm.	obtuse mucro less than 0.5 mm.	obtuse mucro about 0.5 mm.	acute mucro over 0.5 mm.
CAULINE LEAVES				
Length	average 10-13 mm.	average 11-13 mm.	average 16-19 mm.	average 16-19 mm.
Breadth	1-1.8 mm.	1-2 mm.	2-3 mm.	2-3.5 mm.
Apex	acuminate sometimes scarious	acute	acute	acute- acuminate
STAMINATE INVOLUCRE				
Height	3.8-5 mm. average 4.5	3.8-5 mm. average 4.5	5.5-6.5 mm. average 6	5.5-6.5 mm. average 6
Shape of bracts	elliptic acute	broad-elliptic obtuse	broad obtuse	elliptic obtuse-acute
PISTILLATE INVOLUCRE				
Height	5-6.5 average 6	5-7 average 6.2	6.2-7.5 average 7.2	7-8 average 7.5
No. of bracts	25-35	25-35	35-50	30-40
Apex of bracts	obtuse-acute erose	acute-acumi- nate, entire	obtuse-acute entire	acute-attenuate slightly erose
Width of outer bracts	0.8-0.9 mm.	0.7-0.8 mm.	1.1-1.4 mm.	0.9-1.1 mm.
No. of florets	40-65	40-70	70-140	50-100
PISTILLATE FLORETS				
Length of corollas	3.2-4.2 mm. average 3.6	3.5-4.5 mm. average 3.8	4-5 mm. average 4.2	4.2-5.2 mm. average 4.7
Apex of corollas	mostly regular	irregular	regular	irregular
Pappus hairs	remotely barbellate	closely barbellate	closely barbellate	remotely barbellate
PITS OF RECEPTACLE	shallow 0.2 mm. ridges blunt	shallow 0.2 mm. ridges thin, sharp	deep 0.25 mm. ridges blunt	deep, 0.25 mm. ridges thin, sharp

In computing the size of the basal leaves, measurements were taken from the largest leaves of well developed rosettes. The middle cauline leaves only are included in the measurements. The corolla measurements do not include the styles. The apex of the pistillate corolla is considered regular when, as in FIG. 3, its opening is horizontal or nearly so, and the hairs fringing it are about equal in length,

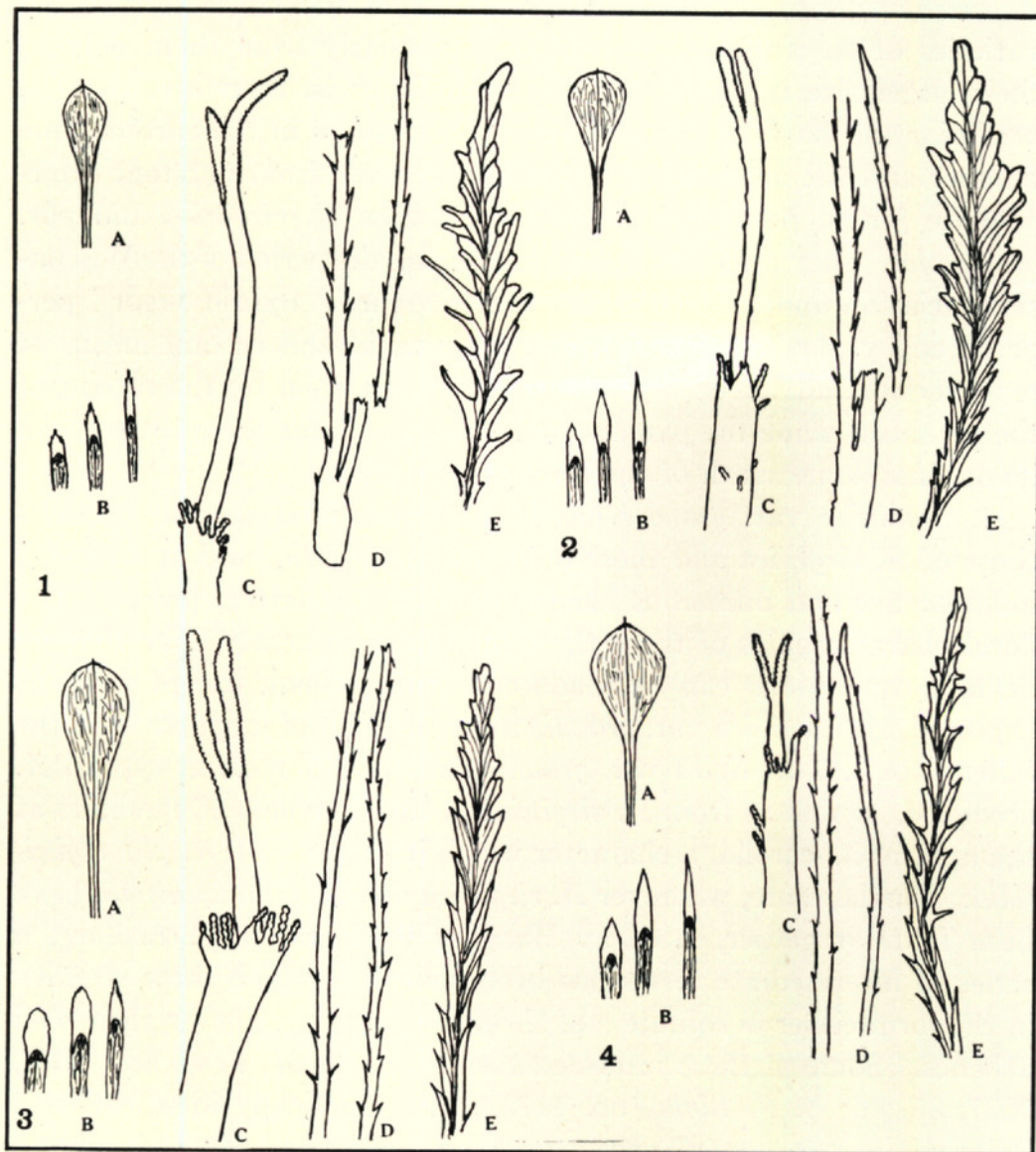


Fig. 1, *ANTENNARIA VIRGINICA*: A, basal leaf, $\times \frac{4}{5}$; B, outer, middle and inner involucral bracts, $\times 2$; C, apex of corolla of pistillate floret, $\times 30$; D, base and apex of pappus-hair of pistillate floret, $\times 30$; E, apex of pappus-hair of staminate floret, $\times 30$.

Fig. 2 (A, B, C, D and E), *A. VIRGINICA* var. *ARGILLICOLA*, same magnifications.

Fig. 3 (A, B, C, D and E), *A. NEODIOICA* var. *TYPICA*, same magnifications.

Fig. 4 (A, B, C, D and E), *A. NEODIOICA* var. *ATTENUATA*, same magnifications.

and irregular when, as in FIG. 4, the opening is oblique, or notched, with the hairs markedly unequal in length, and usually a few are situated on the upper part of the limb. FIG. 2 illustrates the closely barbellate pappus hairs of *A. virginica* var. *argillicola*, while the remotely barbellate hairs of *A. neodioica* var. *attenuata* are shown in FIG. 4. From this chart the fact is apparent that the two varieties of *A. neodioica* show different combinations of the characters of the varieties of *A. virginica*, and differ consistently from them only in their larger size throughout. The probability is, therefore, that *A. neodioica* and its var. *attenuata* arose, by increase in the chromosome number and the acquisition of parthenogenesis, from different intermediate forms, presumably hybrids, between *A. virginica* and var. *argillicola*. They probably originated during the period of the Wisconsin glaciation and, due to their greater vigor, ("hybrid vigor" perpetuated by parthenogenesis), and their rapid and certain means of reproduction, advanced over the territory left open by the retreat of the ice sheet, while the parent species remained, for the most part, in its original home south of the limit of glaciation.

A. neodioica var. *grandis* has basal leaves intermediate between those of *A. virginica* and those of *A. plantaginifolia*, and in its looser inflorescence and numerous heads resembles the latter species. The floral characteristics of these three forms are so nearly alike that no definite conclusions can be made concerning them, except that, as expected, *A. neodioica* var. *grandis* is larger in all of its parts than the other two. *A. neodioica* var. *grandis* usually differs from typical *A. neodioica*, as well as from *A. virginica* in the shortness of the hairs at the apex of its corolla, a character which it shares with *A. plantaginifolia*. Furthermore, wherever *A. virginica* and *A. plantaginifolia* have been found together, *i. e.*, at Hanging Rock and at Strasburg, a series of intermediate forms has been collected, which show sterility in the form either of minute and shrunken pollen grains or shrivelled achenes. Some of these intermediate forms (*W. M. Frye*, nos. 1034, 1037, 35, 36; *S. F. Blake*, no. 11732,) are practically identical with *A. neodioica* var. *grandis* except for their small size. There is a complete series of gradations from *A. virginica* to these intermediate forms, just as there is from *A. neodioica* to var. *grandis*. Hence *A. neodioica* var. *grandis* probably originated from these partially sterile hybrids in the manner previously described. Although var. *grandis* is primarily of a more northerly range, I have seen one specimen (Moon Township, Alleghany County, Pennsylvania, *J. H. Schafer*, no. 262)

clearly of this variety, within the range of *A. virginica*, and some of Frye's collections approach it.

The other two recognized varieties of *A. neodioica*, vars. *chlorophylla* and *interjecta*, are more difficult to explain. Var. *chlorophylla* shows a transition toward *A. canadensis*, not only in the green and glabrous upper surface of its leaves, but in the shape of its basal leaves and of the involucre bracts as well, although agreeing with *A. neodioica* in the absence of appendages on the upper cauline leaves, the height of the involucre, and the length of the corollas. If a plant can be found, and certain specimens that I have seen lead me to believe that it exists, which is the sexual counterpart of *A. canadensis* just as *A. virginica* is of *A. neodioica*, then the origin of both *A. canadensis* and *A. neodioica* var. *chlorophylla* could be explained in the same manner as that of the other eastern American species.

Var. *interjecta* is transitional toward *A. rupicola*, a species which, along with *A. gaspensis*, was formerly considered a variety of *A. neodioica*, but whose specific identity is now clearly understood.¹ Both of these latter species are relic endemics of the region about the Gulf of St. Lawrence, except for the isolated occurrence of *A. rupicola* in the Great Lakes region, and show certain resemblances toward some of the Cordilleran species of *Antennaria*. The likelihood is, therefore, that they have existed since the period before the Wisconsin glaciation, and were evolved at a time when the eastern and the western species of *Antennaria*, now isolated from each other, were mingling together. If this is so, then *A. neodioica* var. *interjecta*, also a relic endemic, of the region about Bic, Que., may be considered a member of this series which approaches more nearly *A. neodioica* and therefore *A. virginica*.

The existence of *Antennaria virginica* is, therefore, further evidence in favor of the hypothesis that the parthenogenetic species of *Antennaria* originated from the sexual species by a process including an increase of the chromosome number and often hybridization.

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¹ Cf. M. L. Fernald, RHODORA 35: 341-343. 1933.



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