

**EVIDENCE FOR A SPECIES-LEVEL DISTINCTION OF
TWO CO-OCCURRING ASTERS:
ASTER PUNICEUS L. AND *ASTER FIRMUS* NEES**

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ABSTRACT

We examined the possibility that two co-occurring wetland asters, commonly referred to as *Aster puniceus* var. *puniceus* and *A. puniceus* var. *firmus*, are sufficiently distinct to be segregated at the species level. In our study of collected and field specimens we limited our research to 10 study sites in southern Michigan where both asters coexist. We assumed that if the two taxa belong to one species, gene flow (and hence, intermediate forms) will most likely occur in locations where they grow together (Wagner & Wagner 1983). By quantifying previously-cited characters and new comparative traits of below-ground parts, above-ground vegetative characteristics and capitulescence architecture, we found no evidence of intergradation between these coexisting populations. Therefore, we conclude that the most appropriate taxonomic treatment of these asters is to recognize a species-level designation: *Aster puniceus* L. and *Aster firmus* Nees.

INTRODUCTION

The notoriously difficult genus *Aster* has provided plant taxonomists fertile ground for inquiry and debate (Jones 1980a, 1980b, 1989; Nesom 1994; Semple et al. 1983, Semple et al. 1996; Shinnars 1941, 1946; Van Faasen 1963; Wiegand 1924). Asa Gray, the renowned 19th century botanist, lamented,

I am half dead with *Aster* . . . If you hear of my breaking down utterly, and being sent to an asylum, you may lay it to *Aster*, which is a slow and fatal poison (quoted in Semple 1987).

Further illustration of the complexity and promiscuity of these taxa has been voiced by Dr. Arthur Cronquist:

If complete morphological discontinuity were the sole criterion for the acceptance of species in this group, they could all be reduced to one species (Cronquist 1943).

Such confusion is well represented in the swamp aster (*Aster puniceus* L.). *Aster puniceus* (sensu lato) is typically classified under the subgenus *Symphotrichum* (Nees) A. G. Jones, section *Salicifolii* Torrey & A. Gray, and subsection *Leucanthi* (Nees) A. G. Jones (Jones 1980a). However, recent taxonomic work suggests the genus *Aster* be separated into 13 distinct genera and that the taxon of this study be classified within the newly proposed genus *Symphotrichum* (Nesom 1994). However, since the foundational literature this study is based upon uses the

older nomenclature, and since the new work cited above has not been widely utilized to date, we will refer to the more traditional names in this paper.

Aster puniceus (sensu lato) is distinguished from other species of *Aster* by several characters: achenes with 3–5(6) ribs; leaves clasping, often strongly auriculate; principal cauline leaves sparsely toothed, gradually tapered toward the base; stem variably hispid; and phyllaries glabrous, eglandular and long-acuminate or attenuate.

When first named, this taxon was not described as exhibiting significant morphological variation. However, as variation has increasingly been recognized, two main subtaxa within *Aster puniceus* have been delineated. One, *A. puniceus* (sensu stricto) has densely hispid stems, purple ray flowers, and a widely spreading capitulescence. The other taxon (which has been variously named) tends to be less hispid, with white ray flowers and a more leafy, crowded capitulescence. Wiegand (1924) recognized the two types and segregated the smooth-stemmed *Aster* as a separate species, *Aster lucidulus* (Gray) Wiegand. However, this taxon had previously been named *Aster firmus* Nees; therefore, *A. firmus* should be the correct name for this taxon when segregated at the rank of species (Jones 1980b).

Yet, the greatest confusion involving these plants is not which species name is most appropriate for the smooth-stemmed *Aster*, but whether or not this taxon truly deserves species-level rank. Many taxonomists include both plants within *Aster puniceus*, recognizing the swamp aster as *A. puniceus* var. *puniceus*, and the smooth-stemmed aster as *A. puniceus* var. *firmus* (Nees) Torrey & A. Gray (Jones 1989, Semple et al. 1983, Semple & Heard 1987, Voss 1996). At least one author (Jones 1984) has separated the taxa at the subspecies level. Others recognize two species (Gleason 1952; Gleason & Cronquist 1991; Jones 1980a, 1980b; Shinnars 1941, 1946; Wiegand 1924), while still others apparently make no distinction below the species level (Britton & Brown 1913; Chmielewski 1987; Semple 1980a, 1980b; Van Faasen 1971, Van Faasen & Sterk 1973).

Authors who do not recognize these two asters as separate species generally appeal to the presence of overlapping characters, suggesting this as evidence of intergradation or even complete lack of discontinuity (Jones 1989; Voss 1996). We evaluated many of these overlapping traits as well as some infrequently cited and novel characters from field and herbarium specimens to ascertain whether morphological discontinuity exists between these asters. Although we did not examine the type specimens, our designations are based upon and consistent with descriptions by Gleason (1952), Gleason & Cronquist (1991), Jones (1980a), Shinnars (1941, 1946), Voss (1996), and Wiegand (1924).

We collected data from both herbarium and field specimens. While it is likely many of the herbarium specimens had come from sites where the two taxa do not co-occur, our field observations were done exclusively at sites where both asters are found in coexisting populations. We predicted that if the taxa are able to cross, introgression would most likely occur at these field sites where the plants exist in proximity (often within one meter of each other). If plants with intermediate traits were found at these locations, we would conclude that these are two varieties of one species. By contrast, if these asters clearly retain their distinctness while living in such proximity, we would conclude that no gene flow is occurring and a species-level designation is warranted (Wagner & Wagner 1983).

METHODS

For this investigation we collected specimens and directly examined living plants from several sites across southern Michigan and analyzed herbarium specimens at the University of Michigan Herbarium (MICH). A total of 22 *Aster puniceus* and 40 *A. firmus* plants were collected from co-occurring populations at seven sites across southern Michigan: Waterloo State Recreation Area (Washtenaw County), Pinckney State Recreation Area (Washtenaw County), Hadley Road (Washtenaw County), Furstenburg Park (Ann Arbor City Park, Washtenaw County), Ives Road Fen (Nature Conservancy Preserve, Lenawee County), Lost Nation State Game Area (Hillsdale County), and Bakertown Fen (Nature Conservancy Preserve, Berrien County). Plants were collected from September to November in 1993, 1994 and 1995. Specimens were pressed, dried, and later examined. Five voucher specimens were deposited at MICH (Warners *A. firmus* 747, 757, 758; *A. puniceus* 756, 745, MICH). All remaining specimens are retained at the Calvin College Herbarium in Grand Rapids, Michigan.

From the collected specimens we quantified rhizome length, leaf midvein pubescence and capitulescence structure, and used these data to graphically illustrate differences. Specimens were collected with as much below-ground material as possible so that various rhizome lengths could be assessed (see Figure 1). Midvein pubescence was measured by averaging hair counts per millimeter of midvein from three leaves per plant under a dissecting microscope. These measurements were taken from the abaxial surface of cauline leaves at an arbitrary location within 3 cm from the base of the leaf. To quantify differences in capitulescence architecture we created a variable, mean BRC (Branching Ratio in the Capitulescence). Mean BRC is the mean ratio of non-flowering to flowering segments (cm) on the three lowermost capitulescence branches (Figure 2).

We also gathered data from living plants in coexisting populations at Warren Townsend Park (Kent County), Pickerel Lake Nature Preserve (Kent County), Flat River State Game Area (Montcalm County), Waterloo State Recreation Area (Washtenaw County), Ives Road Fen (Lenawee County), and Bakertown Fen (Berrien County). Observations were made between 3 July and 30 August 1998. At these sites we collected data for three variables (stem thickness, number of shoots per plant and stem pubescence) from a total of 22 *Aster puniceus* and 28 *A. firmus* plants. Stem thickness was measured at a point 20 cm above the soil surface. The number of living shoots (current year) from the base of a plant was counted after sufficient surface soil was removed to confidently assess which shoots emerged from the same below-ground structure. Stem pubescence was measured by counting the number of hairs (per 25 mm²) on the stem at a point 60 cm above the soil surface.

To assess data from a broader geographical region than southern Michigan, 148 specimens of *Aster puniceus* and 68 specimens of *A. firmus* were examined at MICH by qualitatively evaluating four characters: pubescence in the capitulescence, stem pubescence, pubescence on abaxial surface of leaf midveins, and underground parts. A complete list of citations for each of these specimens may be requested from the authors.

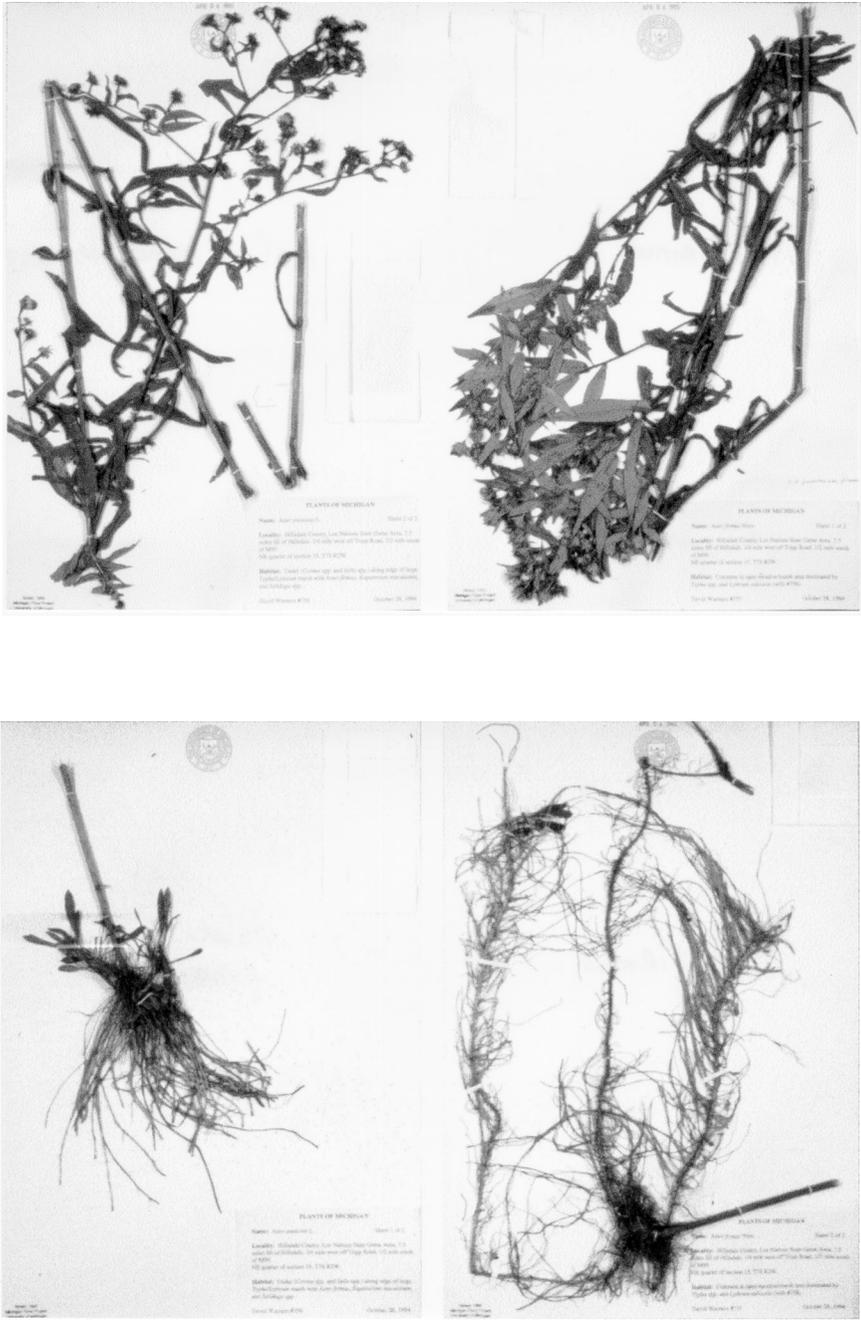


FIGURE 1. Capitulescence and below-ground architectures of *Aster puniceus* (left) and *Aster firmus* (right).

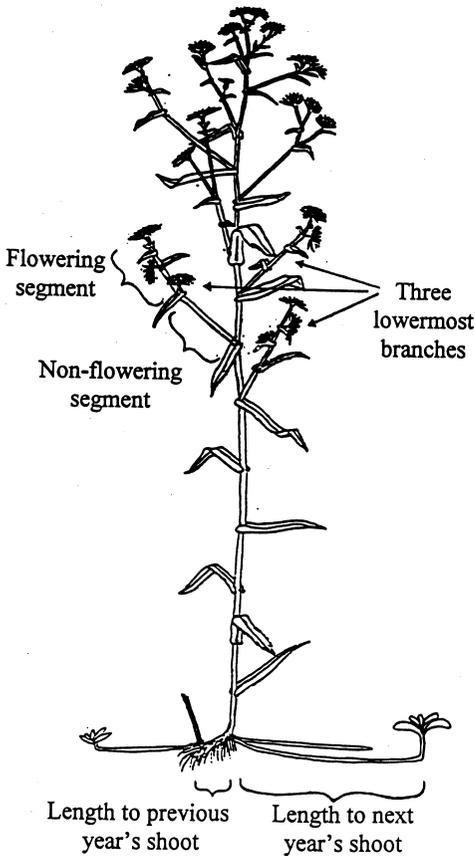


FIGURE 2. Diagram of various characters used to evaluate the two asters from collected specimens. Rhizome lengths were measured in centimeters and mean BRC was calculated by comparing the portions of the capitulescence branches which were flowering and non-flowering (see text for detailed description).

Calculations were done with Microsoft Excel 5.0. The graphs and table were generated using Cricket Graph 1.3 and Microsoft Excel 5.0.

RESULTS

The specimens we collected from coexisting populations exhibited several distinct morphological traits. Figures 1 and 3 illustrate that *Aster puniceus* consistently emerges from a short caudex, while *A. firmus* annually spreads by extended rhizomes. Figure 4 graphically illustrates differences between the taxa using the variables maximum length to next year's shoot, mean BRC, and number of leaf midvein hairs (there are fewer specimens represented in the graphs than the total number collected because we only graphed those specimens that clearly illustrated all the characters analyzed in the graphs). Underground distance to the following year's shoot was always greater in *A. firmus* ($\bar{x} = 29.0$ cm, $sd = 26.6$) than in *A. puniceus* ($\bar{x} = 1.8$ cm, $sd = 1.3$). *Aster puniceus* was found

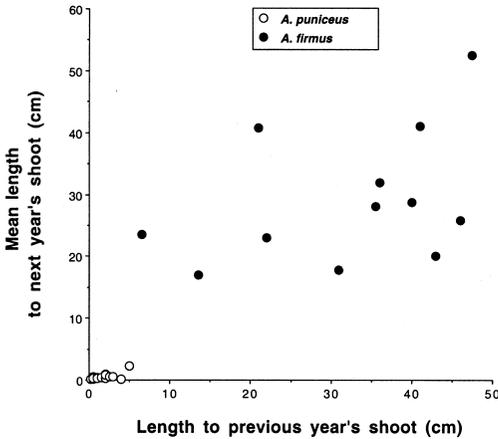


FIGURE 3. A comparison of below-ground structures of the two asters: length to previous year's shoot plotted against the mean length to next year's shoot.

to have variable numbers of cauline leaf midvein hairs ($\bar{x} = 6.8/\text{mm}$, $\text{sd} = 2.3$), while *A. firmus* midveins were typically glabrous ($\bar{x} = 0.14/\text{mm}$, $\text{sd} = 0.37$). The two anomalous individuals (one *A. puniceus* without hairs and one *A. firmus* with hairs) maintained other characters consistent with their taxon. Mean BRC was consistently lower in *A. puniceus* ($\bar{x} = 0.86$, $\text{sd} = 0.39$) than in *A. firmus* ($\bar{x} = 3.38$, $\text{sd} = 1.43$), indicating that the heads of *A. firmus* are much more crowded along the outermost part of the capitulescence.

Observations of living plants in the field yielded additional quantitative data that further delineate the two asters. Figure 5 illustrates these differences using the variables stem thickness (at 20 cm above the soil surface), number of shoots from the base of a plant, and number of stem hairs (per 25 mm² on the stem 60 cm above soil surface). *Aster puniceus* can grow in clumps of several shoots per plant ($\bar{x} = 2.4$, $\text{sd} = 1.6$), whereas we always found *A. firmus* shoots arising singly ($\bar{x} = 1.0$, $\text{sd} = 0$). *Aster puniceus* also commonly displays thicker stems ($\bar{x} = 7.2$ mm, $\text{sd} = 1.5$) than *A. firmus* ($\bar{x} = 4.0$, $\text{sd} = 0.93$) and the stems of *A. puniceus* are more densely pubescent ($\bar{x} = 15.7$, $\text{sd} = 4.5$) than are the stems of *A. firmus* ($\bar{x} = 2.3$, $\text{sd} = 1.9$).

The qualitative data gathered from specimens at MICH illustrate general trends in pubescence differences and further supported differences we had quantified from below-ground material. Four comparisons in pubescence patterns were made (Table 1). Stem and leaf pubescence occurred more commonly and at greater density in *Aster puniceus*. However, pubescence in the capitulescence was found in distinct lines more frequently in *A. firmus*.

We also attempted to compare below-ground material from the MICH specimens (Figure 6). Unfortunately, the majority of herbarium specimens (over 60%) did not include sufficient below-ground material to make such a comparison. However, of those with sufficient root material, the vast majority of *Aster puniceus* specimens exhibited a caudex, and nearly all *A. firmus* specimens had extended rhizomes.

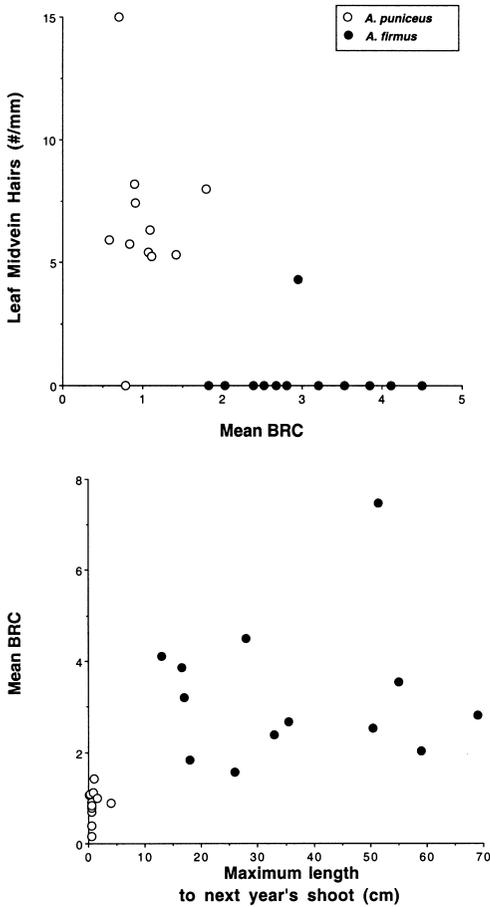


FIGURE 4. Evaluation of below-ground structure, mean BRC, and leaf midvein pubescence from collected specimens. (a) Mean branching ratio in the capitulescence plotted against mean number of hairs on abaxial cauline leaf midvein. (b) Maximum rhizome length to next year's shoot plotted against mean branching ratio in the capitulescence (see Methods).

DISCUSSION

In our evaluation of these plants we have followed two stated lines of advice offered for those who conduct taxonomic research within *Aster*. First, Gleason & Cronquist (1991) and others (Jones 1980b; Semple & Brouillet 1980a; Voss 1996) stress the importance of considering the entire plant body when generating keys or making identifications within this genus. Shinnery (1941) has also raised this concern, emphasizing that "rootstocks are of critical importance." Second, since many of the species within *Aster* are so variable, it has been recommended to use a suite of characters to delineate species, rather than a single or limited number of traits (Carlquist 1976; Cronquist 1943; Semple & Brouillet 1980a).

Several of the traits we used (stem pubescence, capitulescence architecture, leaf midvein hairs) have been used qualitatively by other authors to suggest character overlap (Jones 1989, Voss 1996). However, by carefully quantifying these

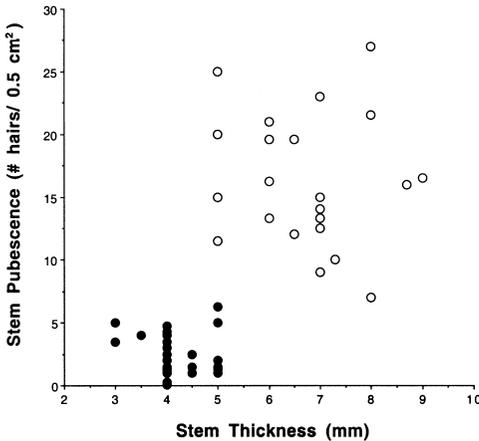
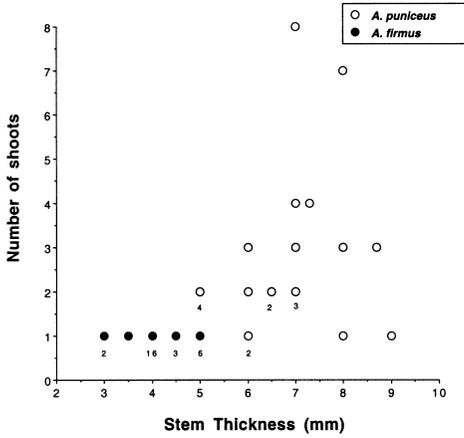


FIGURE 5. Evaluation of stem thickness, number of shoots and stem pubescence from living plants. (a) Stem thickness measured at 20 cm above the soil surface plotted against the number of shoots arising from the base of an individual plant. Points accompanied by numbers represent the number of individuals which shared identical values. (b) Stem pubescence measured at 60 cm above the soil surface plotted against stem thickness measured at 20 cm above the soil surface.

and other traits, we found little evidence of introgression, leading us to suggest these taxa should be classified as two distinct species. The differences we found are particularly noteworthy since we limited our quantitative comparisons to plants that were existing in overlapping populations. If the two *Asters* are of the same species, cross-fertilization and intermediate forms would be expected, especially in areas where the plants co-occur (Wagner & Wagner 1983). Yet we found no evidence that supports the existence of intermediate forms, even though all the plants we evaluated were from coexisting populations.

A comparison of below-ground structures of these *Asters* produced the most significant contrast. The stout caudex of *Aster puniceus* differs markedly from the extended rhizomes of *A. firmus*. We found that *A. firmus* shoots typically produce 2–6 rhizomes beginning in mid to late summer, each eventually reaching between 20–70 cm in length by late fall. To our knowledge these are the longest

rhizomes reported for any species of Michigan *Aster*. In late fall *A. firmus* rhizome tips generally form a leafy photosynthetic rosette at some distance from the “parent” shoot. Late season rosettes are also formed in *A. puniceus*, but due to the absence of rhizomes, they are always found at the immediate base of the current year’s shoot.

This important difference deserves emphasis because it likely influences other morphological traits, including two of our variables, stem thickness and number of shoots at the base of a plant. Although we did not measure stored energy, we predict the type of perennating below-ground structure influences the thickness of a shoot as well as the number of shoots arising at a given point. For instance, while the extended rhizome of *Aster firmus* generally supports only one slender shoot, the stout caudex of *A. puniceus* can support multiple and larger shoots.

These contrasting below-ground structures also give rise to significant ecological differences. Each shoot of *Aster firmus* produces 2–6 new vegetative shoots each generation via extended rhizomes. This means of reproduction allows *A. firmus* to increase in abundance and spread across a suitable habitat during a relatively short time period, even occasionally spreading into drier upland soils. The ability to expand clonally may be a primary reason why *A. firmus* can achieve much higher relative abundance than *A. puniceus*, to the point of being the dominant forb species in some herbaceous wetland communities (Jones 1980b, 1989; Shinnars 1946; Voss 1996; Warners 1997).

By contrast, *A. puniceus* populations are generally comprised of a few distinct individuals, each of which may consist of several shoots, always found in wet, organic soils. While these clumps will slowly increase in size, the increase is very slow and each clump remains stationary, occupying the same immediate location throughout its lifetime. The lower relative abundance of *A. puniceus* compared with *A. firmus*, as well as its more restricted habitat requirements, are likely related to its limited ability to disperse via vegetative propagation.

Specimens from MICH demonstrate that below-ground material is often neglected when collecting these plants. The rhizomes of *Aster firmus* are particularly difficult to remove from the dense sedge meadow root mat in which they typically grow. Since most taxonomic work relies heavily on herbarium specimens, it is not surprising that below-ground structures of these plants have largely been overlooked, and to our knowledge never before quantified.

Other above ground characteristics also help to separate these two asters. Several authors have commented on the more compact, leafy capitulescence of *Aster firmus* and the more open, less leafy capitulescence of *A. puniceus* (Jones 1980b, 1989; Shinnars 1941; Wiegand 1924). Our variable, mean BRC, is the first quantitative description of these contrasting capitulescence architectures. The combinations of a long rhizome with a compact capitulescence in *A. firmus* and a short caudex with an open, lax capitulescence in *A. puniceus* is striking and indicates these two characters likely have a different genetic basis (Brouillet, personal communication).

An infrequently cited character, leaf midvein pubescence (but see Voss 1996), also consistently separates the two species. Stem pubescence is a commonly cited character in comparing these two asters, but many authors have noted how variable this trait can be. We concur that stem pubescence in these taxa is vari-

TABLE 1. Values indicate the percentage of plants that exhibited each trait except for "pubescence on stem," which was scored as either dense or sparse.

Pubescence	<i>A. puniceus</i>	<i>A. firmus</i>
On midvein of cauline leaf	91%	30%
On the stem	80%, dense	85%, sparse
On midvein of capitulescence leaf	80%	13%
In lines in capitulescence	28%	77%

able, yet when we standardized stem pubescence by quantifying stem hairs at a point 60 cm above the soil surface on mature individuals, *A. puniceus* was found to have consistently higher values than *A. firmus*. Stem pubescence is commonly used to compare these plants, and it has been cited both in support of a species-level rank (Jones 1980b; Shinnars 1941, 1946) and as evidence for intergradation (Jones 1989; Semple et al. 1983). This and other often cited overlapping characters (such as ray flower color, head size and habitat preference) are not surprising, given the high variability within many species of *Aster* and the apparently close relationship of these two taxa. These characters illustrate the confusion that can arise when a limited number of morphological traits from a limited portion of the plant body are utilized. We have found stem pubescence to be an important comparative trait, but suggest that it be carefully quantified and used in conjunction with a suite of other characters.

In summary, by standardizing and quantifying traits that previously have been only qualitatively described and by evaluating new characters we find a clear discontinuity between plants here referred to as *Aster puniceus* and *A. firmus*. Our data show clear segregation based upon several unrelated characters and do not support the presence of intermediate forms even though all the plants used in our quantitative analyses were collected from coexisting populations (Wagner &

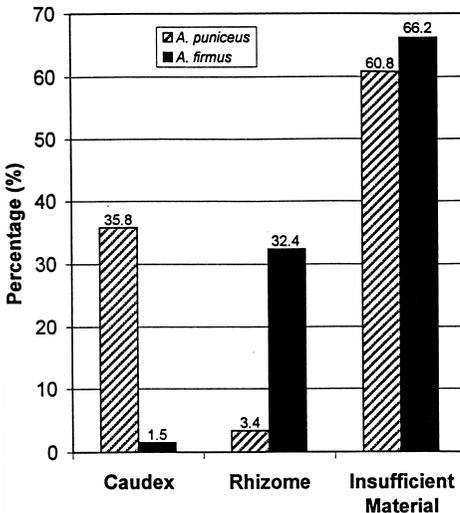


FIGURE 6. Comparison of underground perennating structures from *Aster puniceus* (n=148) and *A. firmus* (n=68) specimens held in MICH. Rhizomes were defined as horizontal stems greater than 5 cm in length. Plants listed in the "insufficient material" category either had no below-ground material or the parts were too incomplete to assess.

Wagner 1983). We conclude that the most appropriate taxonomic treatment of these two asters is a species-level separation.

This study also identifies the need for additional research on these taxa. Our interpretation of the numerous treatments which have failed to recognize a species-level distinction is that a few overlapping characters (stem pubescence, ligule color, and habitat) have been emphasized, while other more definitive characters (particularly below-ground structures) have been overlooked. However, we acknowledge the possibility that these asters behave as distinct species in a portion of their range (including southern Michigan), but may intergrade in other areas, as reported by Jones (1984). Our assessment of herbarium material did not support this phenomenon, but future quantitative research on populations outside the range covered in this study will more confidently evaluate this possibility. Further research that assesses phenotypic plasticity (possibly with additional characters such as capitulescence bract size, capitulescence bract biomass, floral characters, involucre bract traits, etc.) using controlled pollination experiments, as well as molecular techniques, will also contribute to a more detailed understanding of the relatedness of these two asters.

KEY TO ASTER PUNICEUS AND A. FIRMUS

1. Stems densely pubescent, usually purplish; abaxial cauline leaf midvein moderately to densely pubescent; capitulescence widely spreading and heads with lavender to purple ray florets; shoots often found in clumps of 2–6 arising from a persistent stout caudex *Aster puniceus*.
1. Stems glabrous, occasionally hispidulous in lines; abaxial cauline leaf midvein glabrous; capitulescence dense, leafy; heads with white to pale lavender ray florets; shoots arising singly from elongate rhizomes *Aster firmus*.

DESCRIPTIONS OF THE SPECIES

Aster puniceus L. Sp. Pl. 875. 1753.

‘Swamp Aster,’ ‘Purple-stemmed Aster’

Herbaceous perennial with several new shoots emerging annually from a single stout caudex. Stems relatively broad near base (5–11 mm diameter), erect, 50–200 cm tall, usually uniformly anthocyanotic (Semple & Heard 1987). Pubescence on stem densely hirsute, 10–30 hairs per 25 mm²; pubescence in capitulescence moderately dense, occasionally in lines decurrent from nodes. Leaves of winter-rosettes large (Jones 1980b; Gleason and Cronquist 1991), basal leaves commonly deciduous at anthesis. Cauline leaves alternate, 10–22 cm long, 3–4 cm wide at widest point, dark green (Semple 1983), margins crenate-serrate, elliptic to oblanceolate, auriculate clasping; abaxial midvein moderately to densely hispid (5–10 hairs/mm near leaf base). Capitulescence open, lax, panicleiform with widely spreading heads. Leaves in capitulescence

sparse and abruptly reduced in size (50% to 25% size of cauline leaves). Capitula 2–3.5 (4) cm in diameter with rays fully extended. Involucre campanulate, (6) 8–12 (15) mm long (Jones 1989), typically not graduated. Phyllaries slender, long-attenuate, 6–10 (15) mm long, flexible, herbaceous. Ray florets 20–40 (to 60), 12–18(20) mm long, lavender to purple. Disk florets 30–50, narrow but dilated at throat, (4.5) 5–6 mm long, limb turning from cream or yellow to pink or purple after anthesis. Achenes obconic, (2) 2.5–3.5 (4) mm long and 1 mm or less across, 1 rib per side. Pappus a single, simple whorl.

Flowering (late August) September–October. Fruiting October–November. Range extending southward from northeastern states along the Appalachian mountains to Georgia, northwest into Alberta and westward to Nebraska (Semple 1983); most abundant in the eastern part of its range (Semple 1987). Habitat predominantly open to moderately shaded, very wet peat substrate.

Aster firmus Nees. Syn. Ast. 25 (1818).

Syn. *Aster lucidulus* (Gray) Wiegand. *Rhodora* 26: 4 (1924).

‘Smooth-stemmed Aster’

Herbaceous perennial spreading clonally, often forming large colonies. New shoots emerging singly from long, strongly creeping rhizomes (to 70 cm long). Stems moderately thin at base (2–8 mm diameter), erect, 50–200 cm tall, anthocyanotic directly above each node. Basal stem portions often hispidulous, but upper stem (> 30 cm above ground) glabrous with occasional hairs found in decurrent lines from nodes. Leaves of winter rosette small, basal leaves deciduous at anthesis. Cauline leaves alternate, 5–15 cm long, 2–3 cm wide at widest point, typically light green, oblanceolate, auriculate clasping; abaxial midvein glabrous, occasionally hispidulous near tip. Capitulescence densely paniculiform to corymbiform with crowded heads. Leaves in capitulescence slightly and gradually reduced in size from cauline leaves, crowded, at times overtopping heads. Capitula 1.5–3.5 cm in diameter with rays fully extended. Involucre campanulate 6–10 mm long, somewhat graduated. Phyllaries often acute, not strongly attenuate, 6–10 mm long, flexible, herbaceous. Ray florets 20–40, 10–18 mm long, white to pale lavender. Disk florets 30–50, narrow but dilated at throat, (4.5) 5–6 mm long, limb turning from cream or yellow to pink or purple after anthesis. Achenes obconic, 1.7–3.0 mm long and 1 mm or less across, 1 rib per side. Pappus a single, simple whorl.

Flowering Early September–October. Fruiting October–November (Jones 1980b, 1989). Range extending southward from northeastern states along Appalachian mountains to Georgia, northwest into Alberta and westward to Nebraska (Semple 1983); more common in the western part of range (Semple 1987). Habitat predominantly open, wet ground, but prone to spread into mesic mineral soils.

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