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Front Cover

Arisaema macrospathum from Parque Nacional El Tepozteca, Morelos, Mexico. Note the many leaflets and the very large, open spathe from which the long, attenuate spadix emerges symmetrically © Robert Wyatt and Ann Stoneburner

Back Cover

Philodendron 'Bette Waterbury'. Inflorescence in frontal view at anthesis (*Croat 69686*).

A Review of *Arisaema* (Araceae) in North America: Nine species instead of two?

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ABSTRACT

The most recent treatment of North American *Arisaema* recognizes only two species: *A. triphyllum* and *A. dracontium*. Much of the variation, especially in the *triphyllum* complex is attributed to rampant hybridization, for which there is little to no evidence. We provide arguments for recognizing at least nine species, though some of these taxa need verification involving additional fieldwork and DNA sequencing. We arrived at our conclusions based on examination of herbarium specimens (including critical collections made during two never-published doctoral studies), field observations of the species, recent data reported by contributors to iNaturalist, and critical examination of the literature. Within the *triphyllum* complex, we recognize six species: *A. triphyllum*, *A. pusillum*, *A. stewardsonii*, *A. quinatum*, *A. acuminatum*, and *A. sp. nov. A*. Most authors have treated these as subspecies, varieties, or forms, if they have been recognized at all. All are diploid with $n = 28$ except for *A. triphyllum*, which is a tetraploid with $n = 56$. Within the *dracontium* complex, we recognize three species: *A. dracontium*, *A. macrospatum*, and *A. sp. nov. B*. Again, there has been much confusion surrounding these taxa, but only *A. dracontium* is known to be tetraploid with $n = 56$.

Keywords: *Arisaema*, distribution, ecology, hybridization, North America, phylogeny, sex switching, systematics.

INTRODUCTION

Arisaema Mart. is one of the larger genera in the Araceae with about 220 described species (Manudev et al., 2019). The center of diversity is warm temperate Asia, but the genus provides one of the best examples of Oligocene/Miocene floristic links between East Africa, Arabia, the Himalayan region, China, and North America (Renner et al., 2004). The number of species in North America has been the subject of much discussion, with various authors recognizing as few as two or as many as six distinct taxa. The most recent treatment for *Flora North America* by Thompson (2000) returned to much earlier thinking and recognized only two species (*A. triphyllum* (L.) Schott, Common Jack-in-the-pulpit and *A. dracontium* (L.) Schott, Green Dragon).



Figure 1. Purple-spathed morph of *Arisaema triphyllum* from Niquette Bay State Park, Vermont, USA. Note the well-defined light-colored stripes. All photos, except Figures 9 and 13, are courtesy of iNaturalist and used under the Creative Commons Attribution-Non-Commercial (CC BY-NC) license.



Figure 2. Green-spathed morph of *Arisaema triphyllum* from Central Elgin, Ontario, Canada. Note the stout sterile spadix and wide flanges at the top of the spathe tube.



Figure 3. Purple-spathed morph of *Arisaema pusillum* from Lancaster County, South Carolina, USA. Note the sharply defined purple-black interior of the spathe and narrow flanges



Figure 4. Green-spathed morph of *Arisaema pusillum* from Great Falls, Virginia, USA. Note the abrupt transition to darker green on the spathe and narrow flanges.



Figure 5. *Arisaema quinatum* from Birmingham, Alabama, USA. Note the five leaflets and the curved, slender spadix.



Figure 6. Green-spathed morph of *Arisaema stewardsonii* from Rochester, New York, USA. Note the ridged or fluted white stripes on the back of the spathe.



Figure 7. Purple-spathed morph of *Arisaema stewardsonii* from Glastonbury, Connecticut, USA.



Figure 8. *Arisaema acuminatum* from Ichetucknee Springs, Florida, USA. Note the extremely long acuminate tip of the spathe.



Figure 9. *Arisaema* sp. nov. *A* from Argillite, Kentucky, USA. Note the dark purple interior of the spathe with short stripes of white in the throat.

It is surprising there have been few studies of the systematics and phylogeny of these forest perennials, as these plants represent some of the most readily recognizable flowering plants in eastern North America. Moreover, there have been many studies of the population ecology and reproductive biology of these plants focusing on their unusual labile sex determination that enables switching sex from year to year based on size. So rare is this phenomenon that it is estimated to occur in less than 0.01% of known plant genera (Richardson & Clay, 2001).

Working at Cornell University, Donald G. Huttleston completed an M.S. in 1948 and a Ph.D. in 1953 studying *Arisaema*. The principal data from this work, however, were never published. Only a couple of papers recognizing three (Huttleston, 1949) and, later, four subspecies (Huttleston, 1981) appeared, plus a summary and key with photos in *Aroideana*, a publication that focuses on Araceae (Huttleston, 1984).

A similar situation holds for a doctoral dissertation done at the University of North Carolina at Chapel Hill by Miklos Treiber, completed in 1980. This 355-page work includes field observations over the range of three recognized subspecies, uniform garden and growth chamber comparisons of selected morphological characters, crossing experiments, phenological studies, chromosome counts, pollinator observations, and analyses of sexual and asexual reproduction. None of this voluminous information was ever published, though many authors have cited the dissertation (Treiber, 1980).

We believe the relative obscurity of Huttleston's and Treiber's research is part of the reason there is confusion and uncertainty regarding the number of taxa and their relationships, especially within the *triphylllum* complex. Based on our recent field observations, study of herbarium specimens, critical review of reports on iNaturalist, and careful examination of the relevant literature, we have formulated a set of working hypotheses regarding the taxonomy of these plants. Our list of recognized taxa is shown in Table 1. Most of these coincide with the most recent provisional treatment by Weakley (2020) in his online *Flora of the Southeastern United States*.

These hypotheses need to be tested using modern DNA sequencing, which has been applied with success to resolve relationships among other species of *Arisaema* (Renner & Zhang, 2004; Renner et al., 2004; Ohi-Toma et al., 2016). Unfortunately, all these studies used only one sample of *A. triphylllum* without noting further the species or subspecies to which their samples belonged. Recently, Cai et al. (2019) have published the complete plastome sequence of *A. ringens* (Thunb.) Schott, a species known from China, Japan, and Korea that belongs to the same section of the genus as members of the *triphylllum* complex. Here we explain why we propose that nine, rather than two, species of *Arisaema* exist in North America, setting the stage for testing hypotheses regarding the number of species and relationships within the group.

Materials and Methods

Our initial fieldwork has entailed study of local populations of five species: *A. triphylllum*, *A. quinatum* (Nuttall) Schott, *A. pusillum* Nash, *A. stewardsonii* Britton, and *A. dracontium*. We have

carefully noted the habitats in which each occurs and have looked especially for places where the species ranges overlap, indicating that hybridization might be possible. We have also taken a broader look at the occurrence of these plants through examination of herbarium specimens posted online by SERNEC, CNH, and other regional consortia of herbaria. Especially useful in this case, however, was special access to critical vouchers collected by Huttleston (1949, 1981) and held at BH. Similarly, staff at NCU scanned for us voucher specimens associated with the doctoral work of Treiber (1980).

We have also made extensive use of more recent data, primarily images, reported by many contributors to iNaturalist (Heberling & Issac, 2018). Though nearly all these reports are lumped under either *A. triphyllum* or *A. dracontium*, we were able to determine the identity of the taxa using our own set of key characters. These observations were extremely useful in gaining insight into the distribution and ecology of the taxa on a larger scale. Finally, we examined with a critical eye all available literature regarding *Arisaema* in North America, including the unpublished doctoral dissertations of both Huttleston (1953) and Treiber (1980).

RESULTS

We have taken a fresh look at all existing evidence regarding the systematics of *Arisaema* in North America and conclude there are strong arguments for recognizing nine or more species that Thompson (2000) reduced to two in her treatment for *Flora North America*. She argued that numerous intermediate forms exist, but there is little to no evidence for this view, first promulgated by Huttleston (1949, 1981, 1984). Her concern about sympatric ranges is also questionable. Our fieldwork has shown that, even when two species occur at the same site, they are in distinctly different habitats. And her statement that putative hybrid populations exist between the subspecies with $2n = 42$ is based on very few chromosome counts and questionable determinations by Huttleston (1949, 1981).

We do agree with Thompson (1995, 2000) that these taxa should not be treated as subspecies as suggested by Huttleston (1949, 1981, 1984), Treiber (1980), and Gusman & Gusman (2002). We are unsure why previous treatments did not consider the sets of populations distinct species. Except for a questionable wide cross involving *A. stewardsonii* and *A. dracontium* reported by Sanders and Burk (1992), there are no documented cases of hybridization involving any of the species in the *triphyllum* complex. Moreover, Treiber (1980) was unable to produce any hybrids from artificial crosses between these taxa except for *A. stewardsonii* \times *A. pusillum*. The offspring from that cross were weak, and none survived to flowering size. Differences in habitat preferences and flowering phenology also serve as pre-pollination barriers to crossing in natural populations. It is likely that these species are completely reproductively isolated.

Moreover, there are stable, genetically based characters that can be used to identify these plants to species, especially in the fresh state. Taxonomists have placed too much emphasis on the difficulty of identifying herbarium specimens, as three-dimensional and color-related characters that are diagnostic in the field are lost. Nonflowering specimens cannot be identified with certainty in any case.

The nine species we suggest should be recognized can be grouped into two complexes: the *triphylllum* complex with five named species (and one which we informally label *A. sp. nov. A* pending further study) and the *dracontium* complex with two named species (and one which we informally label *A. sp. nov. B* again pending further study). These are shown in Table 1 along with comparisons to Treiber's (1980), Huttleston's (1981), Thompson's (2000), Gusman & Gusman's (2002), and Weakley's (2020) taxonomies. Below we offer descriptions of each of the species that we recognize, along with information related to chromosome numbers, habitat, and range. A diagnostic key is also provided.

KEY TO THE SPECIES OF *ARISAEMA* IN NORTH AMERICA

- 1a.** Leaf with 3–5 leaflets, arranged palmately; sterile spadix 3.5–8 cm long, cylindrical or clavate, included in the spathe [Section *Pedatisecta*] **2**
- 1b.** Leaf with (5–) 7–15 leaflets, arranged pedately on a semicircular axis; sterile spadix 10–30 cm long, S-shaped, attenuate, long-exserted beyond the spathe [Section *Tortuosa*] **7**
- 2a.** Leaflets glaucous beneath at maturity; spathe flange 2–10 mm broad; spathe apex acute to acuminate **3**
- 2b.** Leaflets green beneath at maturity; spathe flange 1–5 mm broad; spathe apex long-acuminate **5**
- 3a.** Leaves (3–) 5-foliolate; spadix slender, 1–2 mm in diameter, curved; spathe hood green, abruptly acute *Arisaema quinatum*
- 3b.** Leaves 3-foliolate; spadix thicker, 4–10 mm in diameter, not curved; spathe hood purple with white stripes or green with white stripes **4**
- 4a.** Spathe hood purple or green with white stripes reaching well above the spadix; spathe flange 5–10 mm broad; spadix clavate *Arisaema triphyllum*
- 4b.** Spathe hood purple with white stripes reaching just above the spadix, with the median stripe extending farther; spathe flange 2–6 mm broad; spadix cylindrical *Arisaema sp. nov. A*
- 5a.** Spathe hood solid purple or green, without stripes; spadix 2–3 mm in diameter; spathe apex acuminate to long-acuminate *Arisaema pusillum*
- 5b.** Spathe hood green or purple with white stripes; spadix 3–5 mm in diameter; spathe apex long-acuminate **6**
- 6a.** Spathe hood strongly fluted, 4–7 cm long; spathe hood green or purple with distinct white stripes *Arisaema stewardsonii*

- 6b. Spathe hood not fluted, 6–8 cm long; spathe hood green with greenish- white stripes.....
..... *Arisaema acuminatum*
- 7a. Spathe tightly enclosing the spadix, 1–1.5 cm broad when unrolled; spathe tube 2–3 cm
long; spathe hood 2.5–3.5 cm long *Arisaema dracontium*
- 7b. Spathe not tightly enclosing the spadix, 2–8 cm broad; spathe tube 2–7 cm long; spathe
hood 3–11 cm long..... **8**
- 8a. Spadix 15–30 cm long, projecting symmetrically from the spathe; spathe tube 6–7 cm
long; spathe hood 8–12 cm long *Arisaema macrospathum*
- 8b. Spadix 12–20 cm long, projecting asymmetrically from the spathe; spathe tube 2–4 cm
long; spathe hood 3–5 cm long *Arisaema sp. nov. B*

SPECIES DESCRIPTIONS

Arisaema triphyllum Common Jack-in-the-pulpit

Plants 4–9 dm tall. Leaves 1–2 (–3), glaucous beneath at maturity. Leaflets 3 (the lateral leaflets undivided, rarely lobed), arranged palmately. Spathe tube length 4–6 cm. Spathe hood purple with white stripes or green with white stripes, 4–7 mm long, apex acute to somewhat acuminate. Spathe flange 5–10 mm broad, horizontal. Spadix thick, 4–10 mm in diameter, clavate, straight. Stomatal guard cell length > 40 μm .

Comments — There is little disagreement that the most common and wide-ranging species of *Arisaema* in North America is *A. triphyllum*, and that it expresses two color morphs: a purple-spathed variant (Fig. 1) and a green-spathed variant (Fig. 2). Commonly, both occur within the same population, and the trait likely has a simple genetic basis. Plants are typically robust, with a clavate spadix overarched by an expanded spathe. Tissue near the veins of the spathe is lighter in color and especially prominent in the purple-spathed morph, which is clearly striped. Populations range from New Brunswick west to southeastern Manitoba and south to the Panhandle of Florida, Louisiana, and east Texas. The species is known to be tetraploid with $2n = 56$ and is most common in mesic forests and bottomlands along, but not in, streams.

Arisaema acuminatum Florida Jack-in-the-pulpit

Plants 6–9 dm tall. Leaves 1–2, green beneath at maturity. Leaflets 3, arranged palmately. Spathe tube length 4–5 cm. Spathe hood green with lighter stripes, 6–8 cm long, apex long-acuminate, outer surface dull green. Spathe flange 1–5 mm broad, revolute. Spadix 4–8 mm in diameter, cylindrical to somewhat clavate, straight.

Comments — Until very recently, *A. acuminatum* Small has been ignored by virtually all plant taxonomists since its description by Small (1903, 1933) more than 100 years ago. Ward (2012),

however, argued that it deserves to be recognized at least at the level of a subspecies or variety, though his reasons seem to make an even stronger case for species status. This species resembles both *A. triphyllum* and *A. pusillum*, differing in having a very long-acuminate spathe, the upper surface of which is dull green and darker than the inner or lower portions (Fig. 8). It occurs in swamps and very wet woods, commonly on basic substrates from at least southeastern Georgia to the southern Florida peninsula and west to east Texas. It is diploid with $2n = 28$. Huttleston (1949, 1981) considered these plants to represent a widely dispersed hybrid swarm produced by extensive crossing of *A. triphyllum* and *A. pusillum*. This seems highly unlikely.

Arisaema pusillum Small Jack-in-the pulpit

Plants 1.5–3 dm tall. Leaves 1–2, green beneath at maturity. Leaflets 3, arranged palmately. Spathe tube length 3.5–5 cm. Spathe hood solid purple or solid green (never striped), 4–5 cm long, apex acuminate. Spathe flange 1–3 mm broad, revolute. Spadix slender, 2–3 mm in diameter, cylindrical, straight. Stomatal guard cell length $< 40 \mu\text{m}$.

Comments — A much smaller and more delicate species, *A. pusillum*, also occurs in two color morphs. In this case, however, the inside of the upper portion of the spathe of the purple-spathed morph is solid and not interrupted with stripes (Fig. 3), whereas the spathe of the green-spathed morph is uniformly green or green with white or light purple stippling (Fig. 4). The spathe is less robust, as is the spadix, which is more cylindrical. Populations range from southeastern Canada west to Minnesota and south to Georgia, Louisiana, and east Texas. All chromosome counts of this species show it to be diploid with $2n = 28$. It is restricted to swamps and very wet forests.

Arisaema quinatum Southern Jack-in-the-pulpit

Plants 4–8 dm tall. Leaves 1–2 (–3), glaucous beneath at maturity. Leaflets (3–) 5, arranged palmately. Spathe tube length 4–5 cm. Spathe hood uniformly green, 3.5–4 cm long, apex obtuse to abruptly acute. Spathe flange 2–5 mm broad, horizontal. Spadix slender, 1–2 mm in diameter, cylindrical, curved toward the mouth of the tube.

Comments — *Arisaema quinatum* is a more southern species with uniformly green coloration of the flowers. The spadix is conspicuously thin and arched compared to other species, though the plants overall may be as robust as *A. triphyllum*. A distinctive feature of most flowering-age plants is the production of five, rather than three leaflets (Fig. 5). It tends to occur in slightly drier upland forest than other species and ranges from southwestern North Carolina and southeastern Tennessee south to Panhandle Florida and east Texas. It is known to be diploid with $2n = 28$.

Arisaema stewardsonii Bog Jack-in-the pulpit

Plants 3–6 dm tall. Leaves 1–2, green beneath at maturity. Leaflets 3, arranged palmately. Spathe tube length 4–7 cm, strongly fluted. Spathe hood green or purple with white stripes,

4–6 cm long, apex long-acuminate. Spathe flange 1–3 mm broad, revolute. Spadix 3–5 mm in diameter, cylindrical, straight. Stomatal guard cell length < 40 μm .

Comments — *Arisaema stewardsonii* is a more northern species with a strongly ridged or fluted spathe tube and a spathe hood that is green with white stripes (Fig. 6) or purple with green stripes (Fig. 7). A plant of bogs and peaty swamps, this species ranges from Nova Scotia west to Minnesota and south to western North Carolina, eastern Tennessee, and northern Indiana. It is diploid with $2n = 28$.

Arisaema. *sp. nov.* A

Plants 3–7 dm tall. Leaves 1–2, glaucous beneath at maturity. Leaflets 3, arranged palmately. Spathe tube length 4–5 cm. Spathe hood purple with white stripes reaching just above the spadix with only the median stripe sometimes reaching the apex, 4–5 cm long, apex acuminate, outer surface dull green. Spathe flange 2–6 mm broad, horizontal. Spadix 4–8 mm in diameter, cylindrical, straight

Comments — The final species of the *triphylllum* complex is what we are informally referring to as *A. sp. nov. A* pending further study and formal description of the species. It has been considered a form of *A. triphyllum* by Fernald (1940), who based his name, *A. atrorubens* Blume forma *zebrinum* (Sims) Fernald, on *Arum triphyllum* L. var. *zebrina* (Sims, 1806). Unfortunately, examination of Sims's plate illustrating this variety reveals the plant is the common purple-spathed morph of *A. triphyllum* and not the form figured by Fernald (1940) in his Plate 1940-2. This taxon has not been recognized by other authors at any taxonomic level. In our view it differs from the typical purple-spathed morph of *A. triphyllum* in lacking the distinctive stripes within the purple portion of the spathe (Fig. 9). Instead, the upper region is nearly solid purple, as in *A. pusillum*, which the plants also resemble in having more delicate floral structure. In some specimens the central stripe may continue to the tip, but the other stripes are shorter. Originally described by Fernald (1940) from a population in Virginia, we have now seen plants from southern Canada and Michigan south to Georgia, Louisiana, and east Texas. Its habitat includes dripping springs and waterfalls, often associated with sandstone or limestone, along rocky creeks or in swampy ground. Again, this species is diploid with $2n = 28$ (based on counts done by Huttleston of specimens he identified as *A. triphyllum* and Treiber identified as *A. triphyllum* ssp. *pusillum* : e.g., D. G. Huttleston 4 at BH).

Arisaema dracontium Green Dragon

Plants 0.6–1.2 m tall. Leaf 1, with (5–) 7–15 leaflets arranged pedately on a semicircular axis. Spathe tube length 2–3 cm. Spathe hood light green, 2.5–3.5 cm long, tightly enclosing the spadix, 1–1.5 cm broad when unrolled. Spadix 10–17 cm long, attenuate, S-shaped, long-exserted from the spathe.

Comments — Turning to the *dracontium* complex, it has long been assumed that there is only a single species involved, *A. dracontium*, which is easily separated from any member of the



Figure 10. *Arisaema dracontium* from Biddle, Kentucky, USA. Note the large number of leaflets and the spathe tightly enclosing the lower portion of the long spadix.



Figure 11. *Arisaema macrospatum* from Parque Nacional El Tepozteca, Morelos, Mexico. Note the many leaflets and the very large, open spathe from which the long, attenuate spadix emerges symmetrically.



Figure 12. *Arisaema* sp. nov. B from Barton Creek, Austin, Texas, USA. Note the many leaflets and the more open spathe from which the long, solid spadix emerges asymmetrically.

triphylum complex. Leaves of this species typically are comprised of 7 to 15 leaflets arranged pedately, rather than palmately, on a semicircular axis. Moreover, the spadices are very long, attenuate, and strongly exerted from the tightly enclosing spathe (Fig. 10). Plants grow in bottomlands and floodplains from southern Quebec, Michigan, and Wisconsin south to northern peninsular Florida and east Texas. This species is tetraploid with $2n = 56$.

Arisaema macrospathum Mexican Green Dragon

Plants 6–9 dm tall. Leaf with (5–) 7–12 leaflets, arranged pedately on a semicircular axis. Spathe tube length 6–7 cm. Spathe hood light green, 8–12 cm long, not enclosing the spadix, 6–8 cm broad when unrolled. Spadix 15–30 cm long, attenuate, S-shaped, projecting symmetrically from the spathe.

Comments — Ward (2012) concluded, as we have, that diploid plants of *A. dracontium* from peninsular Florida are distinct from true *A. dracontium* and described them as a new variety of that species. Unfortunately, he based the name on the specific epithet of a species that occurs in Mexico (*A. macrospathum* Benth.), which is superficially similar in having a reduced number of leaflets and a more open spathe that loosely covers the lower portions of the long, slender, curved spadix (Fig. 11). In contrast, we agree with most taxonomists (e.g., Gusman & Gusman 2002) that *A. macrospathum* is a distinctive species that is endemic to Mexico. It ranges from the border of northern Mexico to its southern border, mostly on mountains above 1,700 m in moist and moderately cool temperate cloud forest. Its chromosome number is $2n = 28$ (Sousa et al., 2014).

***Arisaema* sp. nov. B**

Plants 3–5 dm tall. Leaf with (5–) 7–15 leaflets arranged pedately on a semicircular axis. Spathe tube length 2–4 cm. Spathe hood green, 3–5 cm long, not enclosing the spadix, 2–4 cm broad when unrolled. Spadix 12–20 cm long, solid, S-shaped, projecting asymmetrically from the spathe.

Comments — There has been controversy regarding the ploidy level of *A. dracontium* ever since Huttleston (1949) reported some unexpected counts of $2n = 28$ for some plants from Florida (e.g., *D. G. Huttleston 1022-1* at BH). Boles et al. (1999) also found that plants they sampled from a Florida sinkhole were diploid in contrast to 18 other populations sampled along a transect from Ontario to Louisiana. In our view, these diploid populations represent a second species we are informally designating *A. sp. nov. B* pending more thorough study of these plants from throughout the range. This diploid species tends to be associated with limestone-derived soils and ranges from north-central Florida, where it is most abundant in association with sinkholes, to east Texas. Morphologically, the plants differ from *A. dracontium* in having a more open spathe from which a very long spadix emerges (Fig. 12).

ISSUES NEEDING RESOLUTION

Lack of vegetative characters

Arisaema plants typically produce only one or two leaves per growing season, so there are few vegetative characters for taxonomists to use compared to most other flowering plants. The single leaf of species in the *dracontium* complex is very different in architecture from other North American species, being arranged pedately and divided into many leaflets. These species are most closely related to a group that is primarily Asian (Ohi-Toma et al., 2016). In the *triphylllum* complex, leaves are usually trifoliolate, the three leaflets constituting a terminal and two laterals. There are few differences between species, and even these are subtle for the most part (Weakley, 2020). The contrast between the upper and lower surface is often used to separate *A. triphylllum* and *A. quinatum* from *A. pusillum* and *A. stewardsonii*, the former being described as glaucous (though there is no actual waxy bloom) and the latter as green or lustrous. Sometimes this character is not obvious in dried herbarium specimens or in leaves that are not fully mature.

Five species in the *triphylllum* complex are almost invariably trifoliolate, but occasionally produce a few lobes on the lateral leaflets. But mature flowering *A. quinatum*, as the name implies, typically has five leaflets, one clearly the terminal and the laterals with lobes giving the appearance of additional leaflets. This is complicated, however, by the fact that all of these plants go through a set of ontogenetic stages from unifoliate as seedlings to trifoliolate as adults. It is not uncommon to find even *A. quinatum* flowering while still in the trifoliolate stage. And it is possible to observe all of the intermediate stages in a single clump of plants of this species growing from the cormlets of a single genet. We have also seen very large two-leaved flowering plants of both *A. triphylllum* and *A. pusillum* that appeared to have five leaflets on the primary leaf. It seems that *A. stewardsonii* is least inclined to deviate from being strictly trifoliolate, as observed also by Treiber (1980).

It is unclear why Treiber (1980) decided not to include *A. quinatum* in his study, as earlier collectors had probably regarded it as a separate species more often than any of the other subspecies. Apparently, he observed early in his fieldwork occasional lobes in *A. triphylllum* that approached a quinquefoliate condition (e.g., *Treiber 902* and *Treiber 914* at NCU). He lumped *A. quinatum* in with *A. pusillum*, though his reason for doing so was never explicitly stated. More surprisingly, there are specimens dated as late as 6 June 1978 that Treiber annotated as *Arisaema quinatum* (e.g., *Demaree 52023* at NCU). Perhaps he simply relied on Huttleston (1949), who himself did not formally recognize *A. quinatum* as a subspecies (though he had recognized it at the species level in his dissertation) until after Treiber (1980) had finished his dissertation research (Huttleston, 1981). It is unclear why Thompson (1995) agreed with Treiber (1980) and rejected Huttleston's (1981) recognition of *A. quinatum* as a subspecies. Gusman & Gusman (2002) also followed Treiber (1980), though they never succeeded in getting living 5-foliolate specimens. Ward (2012) in his amplified keys to the flora of Florida, recognized *A. quinatum* as a distinct but rare species.

In any case, leaf characters are also problematic because they may differ depending on the status of the plant as nonflowering, staminate, or pistillate. In his studies, Treiber (1980) did not indicate whether plants he measured for seven morphological characters were sorted by flowering phase. If pooled, this would have artificially increased variability and could be the reason he found no statistically significant differences between the taxa for any of the seven quantitative characters he measured. This is discouraging because in all populations the most common plant sexual phase is nonflowering. Another issue that could have artificially inflated variability is inclusion of plants of *A. quinatum* and *A. acuminatum* in with measurements of *A. pusillum*, given that Treiber (1980) considered these plants to comprise a single subspecies.

Misidentifications based on herbarium material

Fortunately, there are many diagnostic characters of the inflorescences of these species that can be used to separate them, and Treiber's (1980) growth chamber and common garden experiments showed them to be genetically based. These include spathe hood color and striping, spathe tube fluting, spathe tube flange width, and sterile spadix (appendix) shape. A problem arises, however, once fresh inflorescences are pressed and dried for herbarium specimens. The three-dimensional configuration of these structures is lost, as is color. Huttleston (1981) used virtually the same characters as Treiber (1980) and noted plants of the four subspecies are very distinctive and readily identified, at least in living condition. He conceded, however, it is not always possible to identify herbarium specimens to subspecies. This may explain many specimens in herbaria that he assumed might be hybrids and that he annotated with question marks (e.g., *Duncan 9311* at GEO). Later, he stated, most of the distinguishing characteristics are obscured or destroyed by pressing (Huttleston, 1984). Thompson (1995) echoed this view, noting that these morphological forms may be recognizable in the field, but distinguishing these differences on herbarium specimens is often difficult.

Mismatch of ploidy level and identification

It seems likely that both Huttleston and Treiber, like Thompson (1995, 2000), were overly concerned about the impossibility of naming every specimen of *Arisaema* in herbaria. Of Huttleston's work, Treiber (1980) said, although based primarily on herbarium material, Huttleston did consider some ecological factors and provided some cytological data. Unfortunately, some of his chromosome counts and identifications do not match up. For *A. triphyllum* Huttleston (1949) reported that he had made chromosome counts for about 50 plants from various parts of the range. These counts were $2n = 56$ except those for two plants collected at Big Gully, Cayuga County, New York, which had $2n = 28$. Treiber (1980) examined the vouchers for these counts and found that one (*Huttleston 4* at BH) is *A. pusillum*, while the other (*Huttleston 25* at BH) is *A. stewardsonii*. We agree with Treiber's identifications. For the latter two species, Huttleston (1949) reported $2n = 28$ based on 7 and 15 counts, respectively. Later, he reported $2n = 28$ for *A. quinatum* based on counts of 27 plants from Alabama and one from Tennessee (Huttleston, 1981).

Treiber's (1980) own chromosome counts for the *triphyllum* complex were quite extensive and consistent: for *A. triphyllum*, he reported $2n = 56$ based on 64 counts from 25 populations; for *A. pusillum*, $2n = 28$ based on 38 counts from 15 populations; and for *A. stewardsonii*, $2n = 28$ based on 17 counts from 7 populations. As is often the case, stomatal guard cell length was closely associated with ploidy level, averaging $44.5 \mu\text{m}$ for *A. triphyllum*, $33.5 \mu\text{m}$ for *A. pusillum*, and $34.0 \mu\text{m}$ for *A. stewardsonii*. Treiber (1980) speculated that an original ancestral population differentiated into a northern race (*A. stewardsonii*) and a southern race (*A. pusillum*) that hybridized in a remnant area of overlap to give rise to allotetraploid *A. triphyllum*. Huttleston (1949) had proposed this same scenario earlier but rejected it on the grounds that *A. triphyllum* does not combine the characters of the two diploids. Instead, he suggested that the ancestral nexus spawned three separate populations and that the chromosomes in one of them were or became doubled. Being more vigorous, the tetraploid spread more rapidly and more widely than the diploids, according to Huttleston.

A very different story has been told about *A. dracontium*, which also has a wide range in eastern North America (Boles et al., 1999). Chromosome counts from a total of 30 plants revealed that 18 populations were tetraploid with $2n = 56$, but one population from a large sinkhole in Gainesville, Florida was diploid, with $2n = 28$. Boles et al. (1999) concluded that the tetraploid is likely an autopolyploid based on the failure to observe fixed heterozygosity at any of the allozyme loci studied and morphological similarity between plants of the two cytotypes. Plants from the Florida population were highly differentiated genetically (Nei's genetic distance > 0.75) from all other populations sampled along a transect from Ontario, Canada, to Baton Rouge, Louisiana. For all other pairs of populations, genetic distances were < 0.25 . Moreover, the diploid Florida plants were fixed or nearly fixed for unique alleles at two loci (*Skd* and *Pgm*).

Our examination of these diploid plants from Alachua County, Florida, indicates there are morphological differences, such as a larger and more open spathe that does not enclose the spadix, associated with ploidy level and occurrence on limestone. We conclude these plants are an overlooked species that Ward (2012) mistakenly assumed to be identical to a Mexican species and treated as *A. dracontium* var. *macrospatum* (Benth.) D. B. Ward. The first indication these plants might represent a new species can be dated to 1950, when Huttleston obtained unexpected counts of $2n = 28$ for collections from Alachua County. Unfortunately, he never published these observations. Our examination of his voucher specimens (*Huttleston 1019-2* and *1022-1* at BH) revealed plants that match other collections from this site and other sites in Florida. We have also seen plants of similar morphology associated with limestone areas on the Edwards Plateau near Austin, Texas.

Extent of hybridization

In her treatment for *Flora North America*, Thompson (2000) recognized only one taxon in the *triphyllum* complex: *A. triphyllum*. While admitting that different morphological forms may be recognizable in the field, she noted the difficulty of naming herbarium specimens and argued

that there is much overlap in the distinguishing characters. Citing Huttleston (1949, 1953), she stressed the existence of numerous intermediate forms, including hybrids. But the evidence on this issue is extremely thin. Weakley (2020) argued the species are broadly sympatric and sometimes occur together in mixed populations with little sign of introgression or hybridization and seem to behave as biological species.

The only documented study of hybridization involves a wide cross between *A. stewardsonii* and *A. dracontium* at two sites about 1 km apart in floodplain forest along the Connecticut River in Massachusetts (Sanders & Burk, 1992). There are 1,800 putative hybrids at this site, yet such plants have never been seen elsewhere in the broadly overlapping ranges of these two species in the northeastern United States and Canada. Except for height, in which the hybrids outstripped both parents, plants were intermediate for leaflet number, spathe length, and appendix length. Flowering plants of both *A. dracontium* and the hybrids were monoecious, whereas those of *A. stewardsonii* were strictly staminate or pistillate. Sanders & Burk (1992) found staminate hybrids to be sterile and obtained chromosome counts of $2n = 42$ as expected for a triploid.

More recently, Lee et al. (2011) sequenced chloroplast and nuclear ribosomal DNA attempting to confirm the hybrid origin of these plants, but their results were inconclusive. Assuming maternal inheritance of the chloroplast genome, there is some indication that *A. stewardsonii* would have been the maternal parent in this cross. Nevertheless, the overall pattern from the genetic markers did not seem to indicate involvement of *A. dracontium*. It seems odd too that this wide cross should have happened in only one location and only one subspecies of the *triphylum* complex, especially since *A. stewardsonii* is perhaps the most habitat-specific of these taxa. Still, it is certainly possible that these sterile plants could have spread by asexual means over many years to form very large populations at these two sites.

Huttleston (1949) discussed the possibility of hybridization between *A. stewardsonii* and *A. triphyllum* at a site along the Clyde River in New York first mentioned by Wiegand & Eames (1926). Six chromosome counts from putative hybrids showed $2n = 28$ for four and $2n = 42$ for the other two, which would be expected of a triploid hybrid, but nothing is known of the fertility of these plants. Revisiting this subject, Huttleston (1981) did chromosome counts in two populations in northern New York where plants appeared to intergrade. Of 20 plants, three gave counts of $2n = 42$ in the first population. In the second, two of 15 appeared to be triploids.

In discussing *A. quinatum*, Huttleston (1981) pointed out that this taxon should not be confused with Buckley's (1843) *Arum polymorphum*, subsequently transferred to *Arisaema* by Chapman (1860). He believed the latter to represent the product of hybridization between *A. quinatum* and *A. pusillum*, although these plants ranged rather widely from Tennessee to western North Carolina, northern Georgia, and central Alabama. We have examined several of Buckley's specimens, including the holotype (*S. B. Buckley s.n.* at NY), all of which seem to fit clearly into *A. quinatum*. In fact, the specimen cited was annotated by Huttleston himself in 1952 as *A. quinatum*.

Huttleston (1981) also rejected Small's (1903) *A. acuminatum* on the grounds that the populations represented a widely dispersed hybrid swarm involving crosses between *A. triphyllum* and *A. pusillum*. Plants occur along the coast of Georgia and throughout peninsular Florida. Chromosome counts of these plants, however, showed four plants with $2n = 56$ in Georgia and 19 plants from Florida with $2n = 28$. Were these plants actually hybrids, they should be triploids with $2n = 42$. It seems more likely that *A. acuminatum* is a distinct diploid species. We have examined the holotype (*S. M. Tracy 6781* at NY) and additional specimens from Florida and Georgia and think that the plants deserve species status. In any case, it is highly unlikely that these plants represent a hybrid swarm that stretches over two states and achieved this wide distribution spreading by asexual means. Ward (2012) reached a similar conclusion, but treated the Florida plants as *A. triphyllum* var. *acuminatum* (Small) Engl.

It appears to us that the concern with hybridization has been greatly overblown in assessing the taxonomy of *Arisaema*. Even Huttleston (1981) admitted, in spite of apparent hybridization, plants of the four subspecies are very distinctive and readily identified. Treiber (1980) attempted all possible crosses within and among the three subspecies he recognized. His crosses within species gave high fruit-set, ranging from 86 to 90%, but crosses of *A. triphyllum* with either *A. pusillum* or *A. stewardsonii* were completely unsuccessful. Of 245 crosses involving *A. pusillum* as the pollen parent on *A. stewardsonii*, 105 (42.9%) led to fruit-set. Of 343 reciprocal crosses, 159 (46.4%) were successful. Germination of the F1 seeds from these crosses was low, however, averaging 10.6%, and after the first year of growth only 18 corms were recovered. At that point, his growth chambers malfunctioned, ending the experiment prematurely. Treiber (1980) concluded that hybridization between any of these species is very unlikely.

While it is true the ranges of species in the *triphyllum* complex overlap broadly, we reject the view that they intergrade due to hybridization. In our experience, even at sites where two species occur, they are separated ecologically. *Arisaema pusillum* seems to be restricted to the wettest habitats, occurring in swampy areas in deciduous forest, often associated with native species of river cane (*Arundinaria*) in the South. It ranges far to the north, but remains at lower elevations. Although *A. triphyllum* also is associated with moist sites, the plants are generally on streambanks or associated with rich deciduous forest, not in flooded areas. Perhaps the most distinctive habitat is that of *A. stewardsonii*, which occurs in acidic coniferous woods, most often in areas with peat bogs. Its range is more northern than the other species, coming south at higher elevations in the mountains only to North Carolina and Tennessee. Within its more southern range, *A. quinatum* typically is found on drier sites than the other species, though still within deciduous forest. The only species we have regularly found growing in sympatry are *A. pusillum* and "*A. sp. nov. A*," but we have not seen any evidence of introgression. Small's (1903) *A. acuminatum* also grows in wet areas similar to *A. pusillum* and "*A. sp. nov. A*," but in hardwood hammocks dominated by a mixture of palmettos and evergreen hardwoods and on organic soils. *Arisaema dracontium* is most abundant in sandy floodplains of rivers and streams, often under a canopy of deciduous trees. And *A. sp. nov. B* (= *A. dracontium* var. *macrospatum* of Ward (2012)) seems to be associated with limestone soils and especially with sinkholes in Florida. We strongly disagree with Treiber's (1980) characterization of these taxa as ecologi-

cally quite similar.

In contrast, in Asia where species diversity of *Arisaema* is many times greater than in North America, there have been many well-documented reports of hybridization (e.g., at least 15 in Japan *vide* Hayakawa et al. (2010)). And interspecific hybridization has been confirmed in several cases by sequencing of nuclear and chloroplast DNA (e.g., Hayakawa et al., 2011).

Phylogenetic relationships

Studies attempting to clarify the phylogeny of *Arisaema* and related genera in the Araceae have reached similar conclusions. Renner & Zhang (2004) examined biogeography of the *Pistia* clade based on chloroplast and mitochondrial DNA sequences and Bayesian divergence time inference. They included in their sampling *A. dracontium* and *A. triphyllum*, though we are unsure of the exact identity of the latter as the specimen used (*T. Barkman 351* at WMU) was collected in fruit late in the season. It is most likely *A. triphyllum*, but *A. pusillum* also occurs in western Michigan. In any case, it seems that *Arisaema* diversified early enough for two lineages to attain trans-Beringian ranges. *Arisaema triphyllum* groups with *A. amurense* from a predominantly Sino-Japanese clade, whereas *A. dracontium* and *A. macrospatum* group with *A. heterophyllum* from a predominantly Chinese clade. A molecular clock was calibrated based on an 18 million-year-old fossil from the Latah Formation near Spokane, Washington. This fossil was similar to members of the *triphyllum* complex in diameter, shape and striation of the petiole. The resulting timeline suggests that *A. dracontium* and *A. macrospatum* diverged from Asian stock much earlier, perhaps in the Oligocene, and probably arrived in North America long before *A. triphyllum* (Renner et al., 2004).

Ohi-Toma et al. (2016) presented a genus-wide (150 accessions) phylogenetic analysis based on four non-coding regions of the chloroplast genome. They concluded, as Renner et al. (2004) had, that *Arisaema* is monophyletic, but they found serious problems with the sectional classification. Their trees showed *A. triphyllum* in a polytomy within the large Sect. *Pistillata*, and both *A. dracontium* and *A. macrospatum* in a polytomy within Sect. *Flagellarisaema*. It is possible that inclusion of other species of the *triphyllum* complex might prove useful in clarifying relationships within the genus.

Complications related to studies of sex switching

Much attention has been paid to the rare phenomenon of sex switching in populations of *Arisaema* since it was first reported by Schaffner (1922) and most recently reviewed by Lovett Doust & Cavers (1982a). There was an explosion of interest in the 1980s with many studies conducted in the northeastern United States and Canada (e.g., Policansky, 1981; Lovett Doust & Cavers, 1982a; Ewing & Klein, 1982; Bierzychudek, 1982a, 1982b, 1984; Lovett Doust et al., 1986). All of these came to similar conclusions about the basic fact that plants can shift between nonflowering, staminate, and pistillate phases from year to year. The probability of being in a particular phase is related to plant size, regardless of how it is measured, and switching can be altered by manipulation of the resource status of the plant (e.g., removing leaves or

increasing light). Some differences among the studies were apparent, however, in issues such as pollination limiting fruit-set and numbers of seeds per plant. Treiber (1980) found significant differences among the three subspecies he examined with respect to asexual, as well as sexual, reproduction. It has been assumed that all of the studies cited above were done using *A. triphyllum*, but some of the disparities between studies could be due to inclusion of other species of the *triphyllum* complex. This is especially likely, for example, in a study like that of Vitt et al. (2003) where the two populations chosen for comparison were purposely selected because of the contrasting habitats: one from a swamp and the other from a drier deciduous forest.

Because it also exhibits sex switching, *A. dracontium* has also been the subject of several studies. In this case, however, flowering plants are either staminate or monoecious (but with varying numbers of staminate and pistillate flowers (Lovett Doust & Cavers, 1982b)). In both of the populations they studied in southwestern Ontario, there were three times as many staminate as monoecious plants, and the latter averaged twice the size of the former. Clay (1993) also studied size-dependent gender change in this species at the southern limit of its range in Louisiana coming to similar conclusions. He did find, however, that variation in the number of staminate and pistillate flowers of monoecious plants was substantial but generally ranged from 45 to 70% pistillate. Richardson and Clay (2001) surveyed the literature and did extensive field surveys of *A. dracontium* and *A. triphyllum* in southern Indiana. They concluded that species with a sex change pattern like *A. triphyllum* (staminate or pistillate) have more male-biased (79.9%) population sex ratios than do those with a sex change pattern like *A. dracontium* (staminate or monoecious), with population sex ratios averaging 67.3% male. Again, it is possible that some of the disparities between studies is due to inclusion of *A. sp. nov. B*, especially those done in the southern extreme of the range (e.g., Louisiana).

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Table 1. List of taxa in *Arisaema* to be evaluated for possible species status. Comparisons to other taxonomies since 1980 are included. Treiber (1980) and Huttleston (1981) are unpublished doctoral dissertations; Thompson (2000) is the treatment from *Flora North America*; Gusman and Gusman (2002) is a book-length revision of the genus on a worldwide basis; and Weakley (2020) is from an online provisional *Flora of the Southeastern United States*.

Our List	Treiber (1980)	Huttleston (1981)	Thompson (2000)	Gusman & Gusman (2002)	Weakley (2020)
<i>triphyllum</i> complex					
<i>A. triphyllum</i> (2n = 56)	ssp. <i>triphyllum</i>	ssp. <i>triphyllum</i>	<i>A. triphyllum</i>	ssp. <i>triphyllum</i>	<i>A. triphyllum</i>
<i>A. pusillum</i> (2n = 28)	ssp. <i>pusillum</i>	ssp. <i>pusillum</i>	<i>A. triphyllum</i>	ssp. <i>pusillum</i>	<i>A. pusillum</i>
<i>A. stewartsonii</i> (2n=28)	ssp. <i>stewartsonii</i>	ssp. <i>stewartsonii</i>	<i>A. triphyllum</i>	ssp. <i>stewartsonii</i>	<i>A. stewartsonii</i>
<i>A. quinatum</i> (2n=28)	ssp. <i>pusillum</i>	ssp. <i>quinatum</i>	<i>A. triphyllum</i>	ssp. <i>pusillum</i>	<i>A. quinatum</i>
<i>A. acuminatum</i> (2n=28)	ssp. <i>pusillum</i>	ssp. <i>triphyllum</i> × ssp. <i>pusillum</i>	<i>A. triphyllum</i>	ssp. <i>triphyllum</i>	<i>A. acuminatum</i>
<i>A. sp. nov. A</i> (2n=28)	Not Included	Not Included	Not Included	Not Included	Not Included
<i>draconitum</i> complex					
<i>A. draconium</i> (2n=56)	<i>A. draconium</i>	<i>A. draconium</i>	<i>A. draconium</i>	<i>A. draconium</i>	<i>A. draconium</i>
<i>A. macrospathum</i> (2n=28)	Not in Range	<i>A. macrospathum</i>	Not in Range	<i>A. macrospathum</i>	Not in Range
<i>A. sp. Nov. B</i> (2n=28)	Not Included	Not Included	Not Included	Not Included	Not Included