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A bookend in the *Arisaema japonicum* (Araceae) taxonomic debate: morphological and genetic evidence for synonymization

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Abstract

The taxonomic distinction between *Arisaema japonicum* and *A. serratum* has long been contentious, with treatments alternating between recognizing them as distinct species or conspecific variants. To resolve their taxonomic status, we conducted an integrative species delimitation analysis combining detailed morphological assessments with genome-wide single nucleotide polymorphism (SNP) data. Morphological investigations revealed continuous trait variation with numerous intermediates, precluding discrete morphological classification. Coalescent-based phylogenetic inference using Singular Value Decomposition Scores (SVDquartets) failed to recover *A. japonicum* as a monophyletic group, and principal component analysis of SNP data showed no genetic clustering corresponding to species boundaries. Species delimitation using Bayes Factor Delimitation (BFD) overwhelmingly supported a single-species model over competing hypotheses, including those based on previous morphological classifications. Together, these results indicate that *A. japonicum* does not represent a distinct evolutionary lineage and is best treated as conspecific with *A. serratum*. Our findings reconcile morphological and genetic data, providing strong support for the synonymization of *A. japonicum* under *A. serratum*, thereby resolving a longstanding taxonomic ambiguity within the genus *Arisaema*.

Key words: intraspecific variation, monophyly, plant taxonomy, species complex

Introduction

The genus *Arisaema* Martius (1831: 459) contains approximately 200 species (Gusman & Gusman 2006, Tran *et al.* 2022), ranking it among the most species-rich genera in Araceae (Boyce & Croat 2011). The greatest taxonomic diversity is concentrated in temperate and subtropical Asia, with notable diversity also occurring in the African highlands and eastern North America (Tran *et al.* 2022, Ohi-Toma *et al.* 2016). The genus *Arisaema* is characterized by several morphological synapomorphies, including a solitary inflorescence with unisexual flowers, a hooded spathe, and trifoliate to pedately divided leaves that exhibit great diversity in form (Tran *et al.* 2022).

The taxonomic history of *Arisaema serratum* Schott (1832:17) is both extensive and intricate, marked by frequent revisions, synonymizations, and debate over species boundaries. The difficulty in delimiting species within this group stems largely from high levels of morphological variation both within and between populations, as well as substantial overlap in character states with closely related taxa (Table 1). The taxonomic confusion notably includes the distinction of *A. serratum* from *Arisaema japonicum* Blume (1835: 106), a species that itself has acquired at least eight synonyms (Murata *et al.* 2018). Within the *Arisaema serratum* complex, it is not uncommon for new taxonomic descriptions to lack adequate morphological comparisons and suffer from insufficient typification.

Over time, numerous infraspecific taxa—such as *A. serratum* f. *thunbergii* Makino (1901:128)—have been described based on limited or ambiguous morphological traits, including leaf length, which was historically treated as a key diagnostic character despite its known variability of up to 20 cm and sensitivity to environmental conditions

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(Nakai 1934, Yamashiro & Wada 2002). The lack of consistently discrete traits has led to the widespread use of variable, plastic, or environmentally responsive features to define taxa, ultimately contributing to a cycle of taxonomic inflation and subsequent synonymization.

Phenotypic plasticity complicates taxonomy in this group, as morphological traits—particularly those related to leaf form, and spathe patterning—often vary in response to ecological gradients (Royer *et al.* 2009). Compounding this issue is the broad geographic distribution of the *A. serratum* complex across western Japan, where populations are exposed to diverse environmental conditions that may drive clinal variation or local adaptation. Such geographically structured trait variability can mimic the appearance of species boundaries, leading to misclassification of population-level variation as evidence of speciation. As a result, traditional morphology-based approaches have struggled to identify reliable diagnostic characters, and researchers have frequently relied on traits that are either overlapping across taxa or insufficiently informative.

Arisaema serratum has a long history of interspecific treatments with several notable examples throughout the early 20th century. *Arisaema capitellatum* Nakai (1918: 220) was characterized by having large leaves (up to 70 cm), a serrate leaf margin, and spotted petiole (Nakai 1918)—all of which are character states encompassed by the natural variation of *A. serratum*, leading to subsequent synonymization of this taxon (Govaerts 1995). Similarly, *A. niveum* Nakai (1934:780) was differentiated by having variably sized leaflets with raised veins and purple mottles, yet another set of characters differentially expressed in *A. serratum* and leading to subsequent synonymization (Govaerts 1995).

Arisaema japonicum was differentiated from *A. serratum* for having oblong leaflets with an acute apex (as opposed to lanceolate acuminate leaves with uneven serration) and a slightly larger range in leaflet size (Blume 1835). Additionally, the *A. japonicum* inflorescence was characterized as being more robust than *A. serratum*, bearing a leaf with wider leaflets (Blume 1835). The species *Arisaema serratum* var. *japonicum* (Blume) Makino (1912: 1259) was named on a manuscript plate of a specimen inconsistent with other *A. serratum* yet lacking distinct *A. japonicum* features; e.g. a short inflorescence stalk and the absence of spots (Murata & Ohashi 2009). This classified it strictly as a variety of *A. serratum* rather than a form of variation within *A. japonicum*, a taxonomic discrepancy that would remain until later (1920s) reclassifications by Nakai re-elevated the varieties of *A. japonicum* (Murata & Ohashi 2009).

In 1929, Nakai described four taxa segregated from *A. japonicum*: *Arisaema serratum* f. *blumei* Makino (1901: 129), *Arisaema pseudojaponicum* Nakai (1929: 535), *Arisaema pseudojaponicum* f. *serratifolia* Nakai (1929: 535), and *Arisaema takeshimense* Nakai (1929: 535). The descriptions provided for each of these segregations primarily include characters used to distinguish *Arisaema japonicum*: the presence of two leaves with oblong leaflets, entire or serrate margins, an acute tip, and purple-spotted tunicate cataphylls (Nakai 1929). Beyond this, the descriptions of *A. japonicum* segregations are vague or exclude necessary diagnostic information to fully understand their taxonomic validity. In the separation of *A. pseudo-japonicum* f. *serratifolia*, the only character provided is toothed leaf margins, a character known to exhibit a high degree of infraspecific variation with *Arisaema* (Nakai 1929) and even across populations of *A. serratum* and *A. japonicum*. Ultimately, all four segregations were synonymized into *A. japonicum* (Govaerts 1995).

Arisaema japonicum has been variously synonymized with *Arisaema serratum* and other species within *Arisaema* sect. *Pedatisecta* (Schott ex Engler 1879: 541) Gusman & Gusman (2008: 231) based on overlapping morphological traits such as the shape of the spathe and spadix, leaf size, and reproductive characteristics (Murata *et al.* 2018). However, its status as a distinct species has also been periodically reinstated, with researchers proposing that subtle differences in morphology, phenology, and geographical data support its segregation (Murata 2011).

Resolving the taxonomic ambiguity surrounding *Arisaema serratum* and the *A. serratum* complex is critical to understand the involvement of this species in hybrid speciation (Maki & Murata 2001). Such studies rely on precise species delimitation for accurate evolutionary interpretations. Members of the *A. serratum* complex are largely sympatric across western Japan, where they frequently co-occur and share similar flowering periods (Table 1), creating conditions conducive to gene flow. The absence of clear phenological divergence between taxa, such as *A. japonicum* and *A. serratum*, and the lack of strong reproductive barriers raise the possibility of pollen-mediated gene flow and hybridization in natural populations. Unresolved taxonomic boundaries complicate the interpretation of genetic data, particularly in studies exploring introgression and/or hybridization between closely related taxa. Additionally, processes such as Incomplete Lineage Sorting (ILS) and shared ancestral polymorphism can obscure phylogenetic signals, further complicating efforts to delimit species and disentangle patterns of hybridization (Montes *et al.* 2019, Montes *et al.* 2022, Cervantes *et al.* 2023). Clarifying whether *A. serratum* includes multiple cryptic species or represents a single taxon with population-level variation is essential for ensuring that conclusions about hybrid speciation in this group are based on sound taxonomic foundations. This study aims to resolve the taxonomic ambiguity surrounding *Arisaema japonicum* by integrating new morphological and genetic evidence to assess its status as a separate species and ultimately interrogate its role in contributing to the diversity of morphological forms of *Arisaema*.

TABLE 1. Core species tentatively assigned to the *Arisaema serratum* species complex in Western Japan. The revised treatment of *A. japonicum* found in this manuscript is highlighted.

Species	Protologue	Morphological distinction from *A. serratum*	Flowering Phenology	Genetic evidence for species status
A. serratum	Schott 1832	-	Late April–May	N/A
A. japonicum	Blume 1835	Smaller upper leaf (vs leaves of equal sizes); lacks raised spathe veins (vs prominently raised Spath veins).	Late April–May	N/A
A. japonicum	Blume 1835	None.	Late April–May	None
A. ovale	Nakai 1935	Broadly ovate (vs lanceolate) leaflets; fewer leaflets (5–11 vs 10–15); shorter appendix (2/3 the length of the spathe vs ¾ the length of the spathe).	April–May	N/A
A. angustatum	Franchet & Savatier 1878	Sub-linear leaflets (vs lanceolate); spathe limb as broad as tube (vs broader); small stripes on spathe (vs broad stripes)	Late April–May	N/A
A. nikoense	Nakai 1929	Fewer leaflets (5–10 vs 10–15); fewer broad white stripes on spathe (8–12 vs 10–15)	April–May	N/A
A. mayebarae	Nikai 1940	Longer spathe limb (1/3 the length of the spathe vs ¼) at 90° to tube (vs 45°)	April–May	N/A

Materials and methods

Fieldwork was conducted on northwestern Shikoku Island, Japan, from 02 May to 20 May 2024. Five sample locations (Kugawa, Ishizuchi, Kumakogen, Kamigawa, Ozu) were assigned based on the availability of flowering *A. serratum* and *A. japonicum* individuals. Each sample location was at least 30 km apart to capture natural variation among the sampled populations (Fig. 1; Table S1). Sites were further selected to span a range of elevations (200–1200 m) and forest types representative of the broader *A. serratum* complex distribution on Shikoku, with an emphasis on sampling large, established populations to ensure sufficient genetic diversity for downstream analyses. We consider these sites broadly representative of the ecological and geographic range of *A. serratum* on the island.

Individuals at each study site were identified to species using morphological characteristics of both the leaves and inflorescence, following Murata (2011) and Murata *et al.* (2018). Individuals identified as either *A. serratum* or *A. japonicum* (n = 110) were assigned to one of four morphotypes based on diagnostic vegetative and floral characteristics. Individuals with upper leaves as large or larger than the lower leaf and prominently raised abaxial spathe veins were assigned into morphotype T1 (typical of *A. serratum*). Individuals with upper leaves that were ¼ of the size or less of the lower leaf and with flattened abaxial spathe venation were assigned to morphotype T4 (typical of *A. japonicum*). Individuals exhibiting an intermediate expression of these characters were placed into intermediate morphotypes (T2; T3) to assess morphological intergradation between species (Fig. 1).

Fresh leaf tissue of individuals representing morphotypes T1 (*A. serratum* s.s) and T4 (*A. japonicum*) was collected across sample sites and dried in silica (n = 7 ; n = 6, respectively). DNA was extracted following a CTAB protocol (Doyle & Doyle 1987) and size-selected for fragments in the size range of 5–10 kb using SPRI (Solid Phase Reversible Immobilization) SPRI select beads (Beckman Coulter 2012). Genotyping-by-sequencing (GBS) libraries were prepared using the ApeKI restriction enzyme. Library preparation and sequencing were performed at the University of Wisconsin Biotechnology Center DNA Sequencing Facility using an Illumina NovaSeq 6000 to generate 150 bp paired-end reads. Raw sequence data were demultiplexed and processed using Stacks (Catchen *et al.* 2013). All sequence data used in this study were deposited in DRYAD (Scholten & Specht 2025).

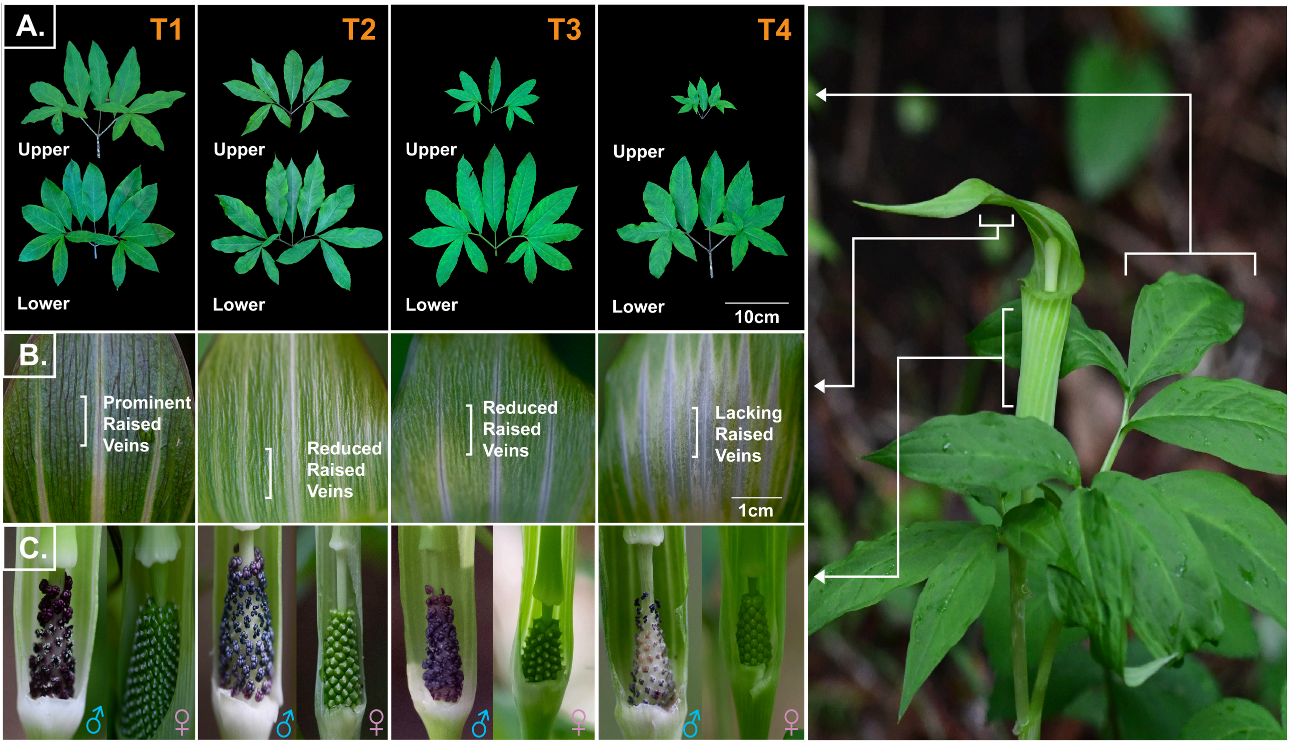

FIGURE 1. Morphological variation of *Arisaema serratum*. A. Leaf size variation in upper and lower leaves; B. Variation in abaxial spathe venation; C. Variation in the flowers of male (♂) and female (♀) inflorescences. T1. Typical *A. serratum* morphotype; T2., T3. Intermediate morphotypes; T4. Typical *A. japonicum syn. nov***.** morphotype.

The sequence data for all individuals was preprocessed using fastp (Chen 2023) and mapped to the draft genome of *A. tosaense* Makino (Scholten 2025) using the Burrow-Wheeler Aligner (BWA-0.07.18) (Li & Durbin 2009). The resulting SAM files were converted into binary format (BAM) and sorted using SAMtools (v1.21) (Danecek *et al.* 2021). Single nucleotide polymorphisms (SNPs) were called and genotyped using GATK (v4.2.0) (McKenna *et al.* 2010). The resulting VCF file was filtered using VCFR (Knaus & Grunwald 2017) and SNPfiltR (DeRaad 2022) to retain variants with a minimum genotype quality of 50% and a minimum read depth of 3, ensuring that only confidently called genotypes supported by sufficient sequencing coverage were included in downstream analyses.

To test for reciprocal monophyly among samples indicative of species delineation, the VCF file was converted into nexus format using vcf2phylip (v2.8) (Ortiz 2019). A coalescence-based phylogeny was generated with SVDquartets (Chifman & Kubatko 2014) with all possible quartets sampled and with 500 non-parametric bootstrap replicates with *Pinellia tripartitea* Schott (1856:5) assigned as the outgroup (Fig. 2).

Species boundaries were further tested using Bayes Factor Delimitation (BFD) (Leaché *et al.* 2014) to compute the marginal likelihood of species trees using the PathSampling algorithm implemented in BEAST2 (Bouckaert *et al.* 2014). Marginal likelihoods were calculated and compared under different species models, including all sampled individuals belonging to the same species (1 species), belonging to prior classification schemes (e.g., Murata 2011) (2 species), and two alternative groupings informed by the coalescence-based phylogeny (2 species). Marginal likelihoods were calculated by sampling 30 steps with the following parameters: 300,000 MCMC steps with 50% burnin and 10,000 pre-burnin steps. These parameters were chosen to conservatively exclude non-stationary samples across power posteriors and ensure accurate model comparison, especially given the sensitivity of Bayes factors to small likelihood differences (Leaché *et al.* 2014). For each species model tested, two independent runs were performed and the average Marginal Likelihood was retained. To further investigate overlapping genetic variation, a principal components analysis (PCA) using SNP data was generated using PLINK (v1.9) (Chang *et al.* 2015) and visualized using Tidyverse (v1.3.0) (Wickham *et al.* 2019) (Fig. 3). Additional admixture analyses were not conducted because the lack of discrete genetic clusters, absence of clear parental reference populations, and limited sample size made such methods neither feasible nor necessary for the species delimitation objectives of this study.

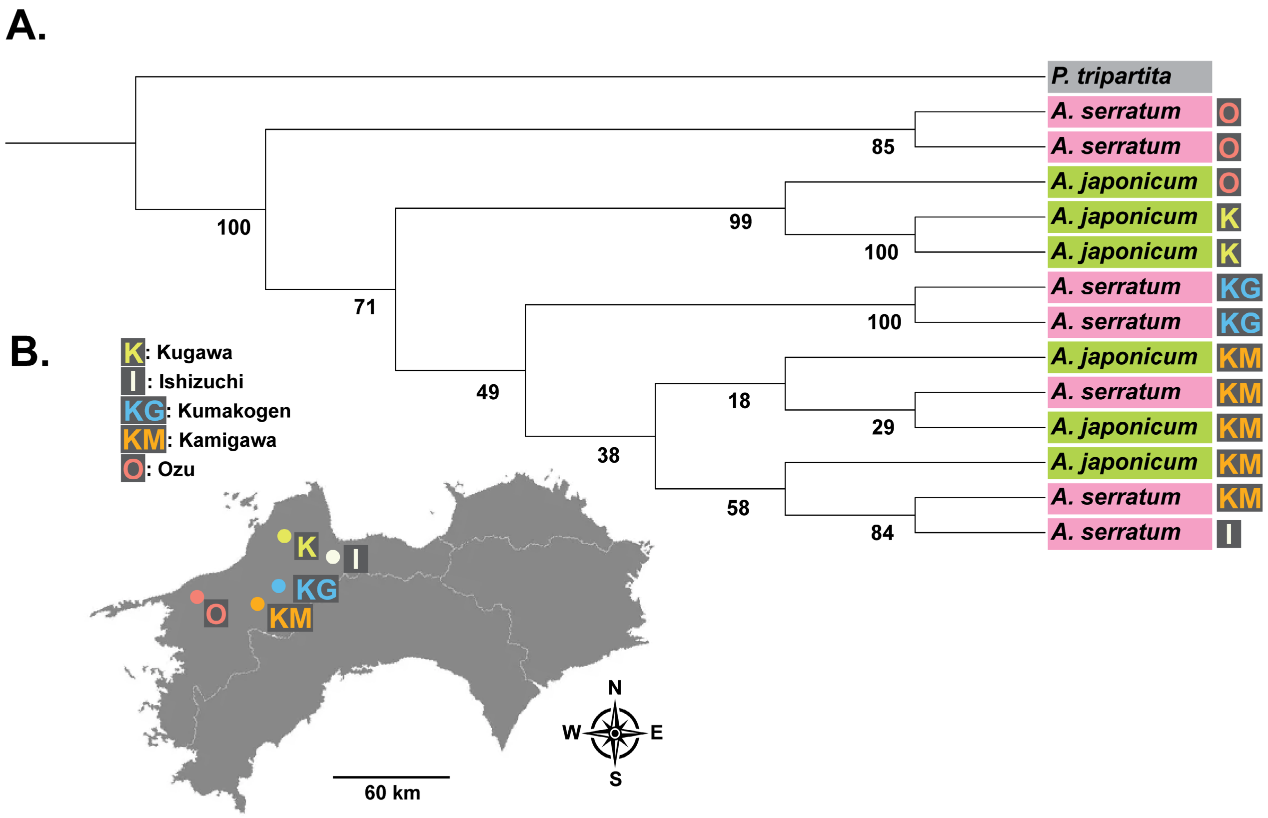

FIGURE 2. Phylogeny of *Arisaema serratum*—*A. japonicum* species complex. A. Coalescence-based phylogeny inferred by SVDquartets, support values represented by bootstrap values. Outgroup: *Pinellia tripartita*; B. An outline of sample locations. Each location is abbreviated according to the legend.

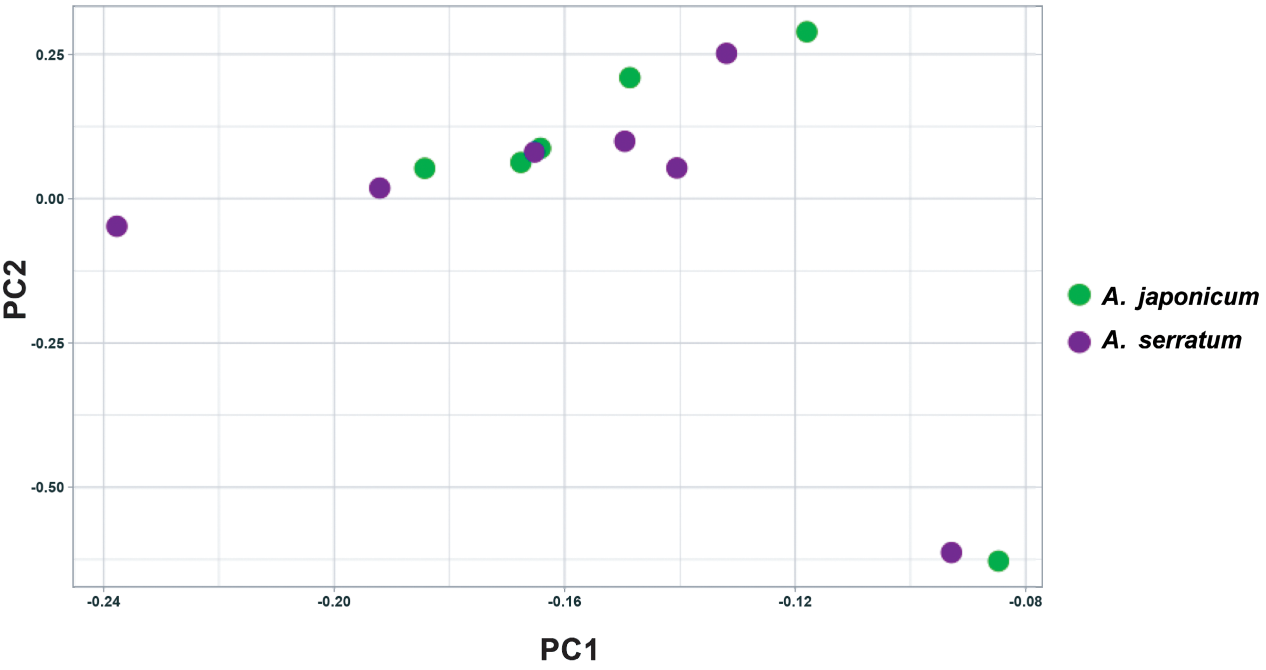

FIGURE 3. Principle component analysis (PCA) of the *Arisaema serratum*—*A. japonicum* species complex using genome-wide SNPs. PC1 explains 26.5% of variation, and PC2 explains 16.3% of variation. Taxa colored according to figure legend: *A. japonicum* (green); *A. serratum* (purple).

Results and discussion

The taxonomic distinction between *Arisaema japonicum* and *A. serratum* has long been controversial, with treatments oscillating between recognizing *A. japonicum* as a distinct species or subsuming it within *A. serratum* as either a variety or a synonym (Murata & Ohashi 2009, Murata *et al.* 2018). The present study provides comprehensive morphological and genetic evidence supporting the synonymization of *A. japonicum* with *A. serratum*, reinforcing historical perspectives that have regarded these taxa as conspecific (Govaerts 1995).

Morphological analyses reveal extensive intergradation between *A. japonicum* and *A. serratum*, challenging their taxonomic separation based on any diagnostic characters or even suites or combinations of traits (Fig. 1). The two primary distinguishing traits of *A. japonicum*—an upper leaf that is significantly smaller than the lower leaf and flattened abaxial spathe venation (Nakai 1929, Murata 2011)—are not consistently distinct from *A. serratum*. Individuals displaying intermediate expressions of these traits were collected across multiple populations (Fig. 1), and no measurable discontinuities in upper leaf size or spathe venation patterns were observed. It should also be noted that an additional phenological distinction used to differentiate between *A. serratum* and *A. japonicum* in the field is the presence (or absence) of emerged leaves at the time of flowering (Murata 2018). This trait was also found to be insufficient in discriminating between the two species, and in fact is a trait known to vary within species of *Arisaema*, likely influenced by environmental conditions (Cook 2004).

Our genetic analyses align with the morphological data in demonstrating a lack of species-level differentiation among collections assigned names of *A. japonicum* or *A. serratum* based on morphotype. Phylogenetic analyses using genome-wide SNPs indicate that *A. japonicum* is not monophyletic, with individuals assigned to *A. japonicum* interspersed within the broader *A. serratum* group. Furthermore, individuals sampled clustered into clades based on geographic location rather than species designation, suggesting that geography and population structure plays a more significant role in genetic differentiation than morphological traits traditionally used to distinguish these taxa (Fig. 2). Such phylogeographic patterns suggest that the putative species do not constitute an independently evolving lineages but rather represent individuals with morphological diversity that falls within the natural genetic variation of *A. serratum*. Likewise, a PCA of genetic data (Fig. 3) reveals no clear genetic clustering that reciprocally separates the two taxa, reinforcing their genetic continuity and indicating ongoing gene flow among the sampled populations and the individuals therein regardless of phenotypic variation.

The results of the Bayes Factor Delimitation analysis further support the synonymization of *Arisaema japonicum* under *A. serratum*. Among the four species tested with the delimitation model, the model that treats all sampled individuals as a single species (rank 1) had the highest marginal likelihood (lnL = -86,570.68), substantially outperforming all alternative two-species models, including those based on previous taxonomic hypotheses and phylogenetic groupings (Table 2). The significantly lower support for the model that separates *A. japonicum* and *A. serratum* following the Murata *et al.* (2011) classification scheme (Model 4, lnL = -129,553.12) strongly suggests that the genetic structure observed across populations does not reflect species-level divergence. Rather, it indicates intraspecific variation within a single evolutionary lineage. This finding is congruent with the PCA analysis (Fig. 3) which reveals no clear genetic clustering segregating the two taxa. Although the observed genetic continuity could reflect either ongoing gene flow or retention of ancestral polymorphism, our data cannot fully disentangle these processes. However, the lack of clear genetic or morphological discontinuities across geographically separated populations suggests that at least some level of contemporary gene flow is likely contributing to the genetic cohesion within these species.

TABLE 2. Summary of species-delimitation models and their respective marginal likelihood values (lnL) tested using BFD. Individuals within the modeled groups are represented by "species abbreviation—sample location (as designated in Fig. 1)".

Species Number	Model	Grouping Rationale	MLE (lnL)	Rank
1	(AJ-O, AJ-K, AJ-KM, AS-O, AS-I, AS-KG, AS-KM)	This paper	-86,570.6776	1
2	(AS-O, AJ-O, AJ-K) + (AS-KG, AJ-KM, AS-KM, AS-I)	Phylogenetic Grouping I	-98,976.5441	2
2	(AJ-O, AJ-K, AS-KG, AS-O) + (AS-I, AS-KM, AJ-KM)	Phylogenetic Grouping II	-121, 583.1189	3
2	(AJ-O, AJ-K, AJ-KM) + (AS-O, AS-I, AS-KG, AS-KM)	Murata *et al.* 2011	-129, 553.1246	4

Given the demonstrated lack of morphological and genetic segregation based on SNP data, the most taxonomically parsimonious conclusion is to subsume *A. japonicum* as a synonym of *A. serratum*. The historical tendency to recognize minor morphological variants within *A. serratum* as distinct taxa (Nakai 1929, 1934, Murata 2011) has likely contributed to taxonomic inflation within this complex. However, as demonstrated in this study, these differences should be carefully assessed first as intraspecific variation rather than evidence of distinct taxa. This work has broader implications for interpreting morphological variation within the *A. serratum* complex and supports the value of applying integrative, genome-wide approaches to resolve other taxonomic ambiguities within *Arisaema*, where high morphological plasticity has historically complicated species boundaries. Future studies combining genomic, morphological, and ecological data could help clarify the circumscription of additional taxa within the *A. serratum* complex, improving the stability and consistency of its taxonomic classification.

Taxonomy

Arisaema serratum (Thunb.) Schott in Schott & Endlicher, *Melet. Bot.*: 17. 1832 (Schott & Endlicher 1832)

= *Arum serratum* Thunb., *Trans. Linn. Soc. London* 2: 338. 1794 (Thunberg 1794).
= *Arisaema capitellatum* Nakai, *Bot. Mag. Tokyo* 32: 220. 1918 (Nakai 1918).
= *Arisaema niveum* Nakai, *Bot. Mag. Tokyo* 48: 780. 1934 (Nakai 1934).
= *Arisaema japonicum* Blume, *Rumphia* 1: 106. 1835 (Blume 1835).

For further synonyms, see Murata & Ohashi (2009).

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TABLE S1. Core species tentatively assigned to the *Arisaema serratum* species complex in Western Japan. The revised treatment of *A. japonicum* found in this manuscript is highlighted.

Site (Ehime Prefecture, Japan)	Abbreviation	Coordinates
Kugawa	K	N 33.8802°, E 132.8547°
Ishizuchi	I	N 33.7756°, E 133.1206°
Kumakogen	KG	N 33.6702°, E 132.9087°
Kamigawa	KM	N 33.6002°, E 132.8707°
Ozu	O	N 33.5193°, E 132.3856°