

An updated genus-wide phylogenetic analysis of *Arisaema* (Araceae) with reference to sections

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Arisaema has a long and complicated taxonomic history regarding its infrageneric classification. In the latest system, 14 sections were recognized, based on an unpublished, tentative phylogenetic analysis; in addition the type species and nomenclatural priority for each section were confirmed. Here, we present an updated, genus-wide phylogenetic analysis, based on four plastid non-coding regions (3'*trnL-trnF*, *rpl20-5'rps12*, *psbB-psbH* and *rpoC2-rps2*) for > 150 accessions. The maximum parsimony and maximum likelihood phylogenetic analyses identified eight major clades and one branch with unique sequence variation, although the relationships were unclear due to a polytomy and weak support. In the phylogenetic trees, most of the sections proposed in the latest system were distinct and corresponded to the major clades, but some sections are not monophyletic. On the basis of the phylogenetic relationship: (1) *A. schimperianum* is treated as a member of section *Arisaema*, rather than section *Tenuipistillata* or section *Sinarisaema*; and (2) section *Fimbriata*, which was synonymised into section *Attenuata* in the latest system but is morphologically distinct from the other species, is redefined as a monotypic section. In conclusion, we recognize 15 sections of *Arisaema* and species-level classifications are discussed in a phylogenetic context. © 2016 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016, 182, 100–114

ADDITIONAL KEYWORDS: chloroplast DNA – infrageneric classification – molecular phylogeny.

INTRODUCTION

Arisaema Mart. (Araceae) is a genus of tribe Arisaemateae, with *Pinellia* Ten. (Keating, 2004), and is related to genera of tribe Areae (e.g. *Typhonium* Schott) in subfamily Aroideae (Renner & Zhang, 2004; Cabrera *et al.*, 2008). *Arisaema* contains nearly 200 taxa of deciduous or evergreen perennial herbs with a single spathaceous inflorescence and one or a few foliage leaves that emerge from an underground stem. Most species are distributed in subtropical to cool temperate regions of Asia and several species are endemic to North America and tropical East Africa (Gusman & Gusman, 2006; Murata, 2011).

The infrageneric classification of *Arisaema* has a long and complicated taxonomic history, including nomenclatural problems (reviewed by Murata, Nagamasu & Ohashi, 2013; Table 1). After Martius (1831)

described *Arisaema*, Schott (1860) grouped all *Arisaema* spp. known at that time into four major groups (*Trisecta* Schott, *Pedatisecta* Schott, *Radiatisecta* Schott and *Peltatisecta* Schott), but these names were not published validly (not shown in Table 1). Subsequently, sections and unranked infrageneric groups have been recognized by various authors (e.g. Engler, 1920; Nakai, 1950; Hara, 1971; Murata, 1984, 1991) and some have even been treated as separate genera (Nakai, 1950). Gusman & Gusman (2002) extensively reviewed the morphological, cytological and ecological characteristics of *Arisaema* and proposed 14 sections as a modification of the system proposed by Murata (1984, 1991). Later, Gusman & Gusman (2006) updated their earlier work by recognizing a total of 15 sections with four additional subsections.

More recently, different sectional classifications were adopted by revisions of the species in China (Li, Zhu & Murata, 2010; not shown in Table 1) and Japan (Murata, 2011), respectively. In particular,

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Table 1. Comparison of the infrageneric classifications of the genus *Arisaema* after Schott (1860)

Engler (1920)	Nakai (1950)	Hara (1971)	Murata (1984; 1991)	Gusman & Gusman (2002)	Gusman & Gusman (2006)	Murata (2011), Murata <i>et al.</i> (2013)
§ 9. <i>Decipientia</i>		<i>Decipientia</i> , comb. inval.	<i>Decipientia</i>	<i>Decipientia</i>	<i>Decipientia</i>	<i>Decipientia</i> (Engl.) H.Li [<i>A. decipiens</i> Schott]
(§ 5. <i>Clavata</i>)		<i>Dochafa</i>	<i>Dochafa</i>	<i>Dochafa</i>	<i>Dochafa</i>	<i>Dochafa</i> (Schott) H.Hara [<i>A. flavum</i> (Forssk.) Schott]
§ 10. <i>Tenuipistillata</i>		<i>Tenuipistillata</i>	<i>Tenuipistillata</i>	<i>Tenuipistillata</i>	<i>Tenuipistillata</i>	<i>Tenuipistillata</i> (Engl.) H.Hara [<i>A. jacquemontii</i> Blume]
(§ 5. <i>Clavata</i>)			<i>Sinarisaema</i>	<i>Sinarisaema</i>	<i>Sinarisaema</i>	
	<i>Sinarisaema</i>	<i>Sinarisaema</i>				<i>Sinarisaema</i> Nakai [<i>A. formosanum</i> Hayata]
		<i>Exappendiculata</i>	Subsection <i>Exappendiculata</i>	Subsection <i>Exappendiculata</i>	Subsection <i>Exappendiculata</i>	
			(<i>Clavata</i>)	(<i>Clavata</i>)	(<i>Clavata</i>)	
§ 8. <i>Speciosa</i>		<i>Trisecta</i>	<i>Trisecta</i>	<i>Arisaema</i>	<i>Arisaema</i>	<i>Arisaema</i> [<i>A. speciosum</i> (Wall.) Mart. ex Schott]
§ 15. <i>Lunata</i>						
§ 14. <i>Wallichiana</i>					Subsection <i>Trisecta</i>	
§ 6. <i>Franchetiana</i>		<i>Franchetiana</i>	<i>Franchetiana</i>	<i>Franchetiana</i>	<i>Franchetiana</i>	<i>Franchetiana</i> (Engl.) H.Hara [<i>A. franchetianum</i> Engl.]
(§ 4. <i>Auriculata</i>)				(<i>Clavata</i>)	(<i>Clavata</i>)	
(§ 4. <i>Auriculata</i>)		(<i>Tortuosa</i>)		<i>Anomala</i> , nom. nud.	<i>Anomala</i>	<i>Anomala</i> Gusman & L.Gusman [<i>A. anomalum</i> Hemsl.]
§ 2. <i>Attenuata</i>		<i>Attenuata</i> , comb. inval.				<i>Attenuata</i> (Engl.) H.Li [<i>A. laminatum</i> Blume]
§ 3. <i>Barbata</i>						
§ 1. <i>Fimbriata</i>		<i>Fimbriata</i> , comb. inval.	<i>Fimbriata</i>	<i>Fimbriata</i>	<i>Fimbriata</i>	
(§ 7. <i>Tortuosa</i>)	<i>Flagellarisaema</i>	<i>Flagellarisaema</i>	Subsection <i>Flagellarisaema</i>	<i>Flagellarisaema</i>	<i>Flagellarisaema</i>	<i>Flagellarisaema</i> (Nakai) H.Hara [<i>A. thunbergii</i> Blume]
§ 4. <i>Auriculata</i>						(<i>Nepenthoidea</i>) (<i>Flagellarisaema</i>)
	<i>Heteroarisaema</i>					
§ 7. <i>Tortuosa</i>	<i>Tortuosa</i>	<i>Tortuosa</i>	<i>Tortuosa</i>	<i>Tortuosa</i>	<i>Tortuosa</i>	<i>Tortuosa</i> (Engl.) Nakai [<i>A. tortuosum</i> (Wall.) Schott]
(§ 2. <i>Attenuata</i>)		(<i>Sinarisaema</i>) (<i>Attenuata</i>)		Subsection <i>Attenuata</i>	<i>Attenuata</i>	<i>Odorata</i> J.Murata [<i>A. odoratum</i> J.Murata & S.K.Wu]
		(<i>Arisaema</i>)		<i>Lobata</i> , nom. nud.	<i>Lobata</i>	
			<i>Pedatisecta</i>	<i>Pedatisecta</i>	Subsection <i>Pedatisecta</i>	
§ 11. <i>Pistillata</i>	<i>Pistillata</i>	<i>Pistillata</i>		Subsection <i>Pistillata</i>	Subsection <i>Pistillata</i>	<i>Pistillata</i> (Engl.) Nakai [<i>A. serratum</i> (Thunb.) Schott]
	<i>Colocasiarum</i>					
§ 13. <i>Ringentia</i>	<i>Ringentiarum</i>				Subsection <i>Ringentia</i>	
(§ 4. <i>Auriculata</i>)			(<i>Sinarisaema</i>)			
(§ 11. <i>Pistillata</i>)		(<i>Pistillata</i>)				
§ 12. <i>Nepenthoidea</i>		<i>Arisaema</i>	<i>Arisaema</i>	<i>Nepenthoidea</i> , stat. inval.	<i>Nepenthoidea</i> , stat. inval.	<i>Nepenthoidea</i> (Engl.) Gusman & L.Gusman [<i>A. nepenthoidea</i> (Wall.) Mart. ex Schott]
§ 5. <i>Clavata</i>			<i>Clavata</i>	<i>Clavata</i>	<i>Clavata</i>	<i>Clavata</i> (Engl.) H.Obashi & J.Murata [<i>A. clavatum</i> Engl.]
		(<i>Tortuosa</i>)		(<i>Tortuosa</i>)	(<i>Tortuosa</i>)	
(§ 5. <i>Clavata</i>)			(<i>Clavata</i>)	(<i>Clavata</i>)	(<i>Clavata</i>)	(<i>Tenuipistillata</i>)

Sectional names are indicated, but names with a symbol '§' in Engler (1920) represent an unranked group. For repeated names in each system, names including non-type species are indicated in parentheses. Blanks represent unconsidered or untreated taxa. Bold italic names in Nakai (1950) indicate genera. Murata (1991) split section *Arisaema sensu* Murata (1984) into two sections: *Arisaema* and *Pedatisecta*. In Murata (2011), section *Odorata* is a nomen nudum, which was then legitimately published by Murata *et al.* (2013). In Murata (2011) and Murata *et al.* (2013), the author of section is provided and the type species of each section is also indicated in angled brackets.

Murata (2011) reconsidered the type species and nomenclatural priority of each section and proposed a new sectional classification with reference to an unpublished, tentative molecular phylogenetic analysis (Table 1). Finally, Murata *et al.* (2013) proposed a revised infrageneric classification, consisting of 14 sections, including the legitimate publication of

section *Odorata* J.Murata. Murata *et al.* (2014) revised the Chinese species according to the system of Murata *et al.* (2013).

In contrast to the extensive history of the infrageneric classification, molecular phylogenetic analyses of *Arisaema* are still insufficient. Most recently, Renner, Zhang & Murata (2004) conducted

phylogenetic analyses, based on the *3'trnL-trnF* sequences of 81 accessions (aligned sequence length 459 bp) that represented 77 species and covered the whole geographic range of the genus. Their phylogenetic tree indicated that *A. tortuosum* (Wall.) Schott, a Himalayan species in section *Tortuosa* Engl., was the first to branch off in the genus, but the remaining taxa mostly formed a polytomy. Renner *et al.* (2004) conducted additional analyses of *3'trnL-trnF* and *rpl20-5'rps12* (total aligned sequence length c. 1300 bp) for 45 accessions and the same regions plus the *trnL* intron (total aligned sequence length c. 2000 bp) for 27 accessions. Their results did not support the monophyly of seven of the sections proposed by Murata (1984, 1991): sections *Arisaema*, *Clavata* Engl., *Fimbriata* Engl., *Franchetiana* Engl., *Pedatisecta* Engl., *Sinarisaema* Nakai and *Tortuosa*. In addition, the phylogenetic tree revealed an unexpectedly close relationship between *A. schimperianum* Schott, a species with radiate leaves from Africa, and *A. costatum* (Wall.) Mart. ex Schott, a species with trifoliolate leaves from the Himalayas, which are geographically distant and have been morphologically classified into different sections. The resolution of the phylogenetic trees was insufficient, however, due to a lack of phylogenetic information and the low level of taxon sampling, precluding further discussion of infrageneric classification.

In the present study, we aimed to assess the sectional classification of *Arisaema* on the basis of a more extensive molecular phylogenetic analysis and to verify the results of Renner *et al.* (2004), i.e. the early branching position of *A. tortuosum* in the genus and the close relationship between *A. schimperianum* and *A. costatum*. To accomplish this, we utilized some of the available DNA samples used by Renner *et al.* (2004), in addition to collecting dozens of new samples, especially those from the Sino-Japanese floristic region, and analyzed these using four plastid non-coding regions (*3'trnL-trnF*, *rpl20-5'rps12*, *psbB-psbH* and *rpoC2-rps2*).

MATERIAL AND METHODS

TAXON SAMPLING

In total, 156 samples from 138 taxa (124 species, 11 subspecies, two varieties and one unknown species from Myanmar) of *Arisaema* were used for the phylogenetic analyses (Appendix). Of these, 37 were DNA samples previously used by Renner *et al.* (2004) and were supplied by Dr S. S. Renner, one was *A. serratum* (Thunb.) Schott nucleotide sequences of which were analyzed by Ohi-Toma *et al.* (2010) and 118 plants were newly collected from natural populations

and cultivations. To verify the early branching position of *A. tortuosum* and the close relationship between *A. costatum* and *A. schimperianum*, we collected new living materials of the three species. The samples covered all the sections and included most of the type species of the sections proposed by Gusman & Gusman (2006) and Murata (2011). The type species of sections *Anomala* Gusman & L.Gusman (*A. anomalum* Hemsl.) and *Odorata* (*A. odoratum* J.Murata & S.K.Wu), however, were not collected, owing to their rarity. In addition, *Pinellia pedatisecta* Schott and *P. tripartita* (Blume) Schott, nucleotide sequences of which were determined by Ohi-Toma *et al.* (2010), were used as outgroups.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

For the newly obtained samples, total genomic DNA was extracted from silica gel-dried leaf tissue using the HEPES-CTAB method described in Ohi-Toma *et al.* (2010). For 155 samples (excluding *A. serratum* and two *Pinellia* spp.), nucleotide sequences of *3'trnL-trnF* (Taberlet *et al.*, 1991), *rpl20-5'rps12* (Hamilton, 1999), *psbB-psbH* (Xu *et al.*, 2000) and *rpoC2-rps2* (Kitano *et al.*, 2005) were determined by direct bidirectional sequencing following the polymerase chain reaction (PCR). Amplification was conducted using *TaKaRa ExTaq* polymerase (TaKaRa Bio, Shiga, Japan), and the following cycling conditions: denaturation at 96 °C for 45 s, followed by 33 cycles at 96 °C for 45 s, annealing at 50 °C for 45 s, extension at 72 °C for 1 min, and a final extension at 72 °C for 10 min. The following primers were used for PCR amplification: (1) e (5'-GGTTCAGTCCCTCTATCCC-3') and f (5'-ATTTGAACTGGTGACACGAG-3') of Taberlet *et al.* (1991) for *3'trnL-trnF*; (2) *rpl20* (5'-TTTGTTCTACGTCCTCCGAGC-3') and 5'-*rps12* (5'-GTCCAGGAACATGTACTAGG-3') of Hamilton (1999) for *rpl20-5'rps12*; (3) the forward (5'-GATTAGCAATCCGCGCTTT-3') and reverse (5'-TTACCAC-TAACTATACCCGC-3') primers of Xu *et al.* (2000) for *psbB-psbH*; and (4) *rps2*-Ty (5'-TCCTAGTACCATGACC-3') of Ohi-Toma *et al.* (2010) and the reverse primer (5'-CGAGTTTTAGCAAAGCTGC-3') of Kitano *et al.* (2005) for *rpoC2-rps2*. Amplification products were purified using the GeneClean III DNA Purification Kit (BIO 101, Carlsbad, CA, USA) or ExoSAP-IT (GE Healthcare UK Ltd., Buckinghamshire, UK). The purified PCR fragments were amplified using the Big Dye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA). Cycle sequencing reactions were performed using the same primers for the PCR amplification; for *rpl20-5'rps12*, the following sequencing primers were also used: *rpl20*-300F (5'-GATTCCTTCGTTTC-TATGGT-3') and *rps12*-300R (5'-

AGAGAGGACCTCVCCGTTT-3') of Ohi-Toma *et al.* (2010). Complementary strands of the sequenced regions were assembled and edited using ATGC v.4.2 (GENETXY Co., Tokyo, Japan). All newly generated nucleotide sequences were deposited in the DNA Data Bank of Japan (DDBJ), linked to GenBank, and their accession numbers (AB982302–AB982921) are shown in the Appendix. In addition, nucleotide sequences of *A. serratum* (source: Ohi-Toma, Arisa222) and two *Pinellia* spp. (outgroups), deposited by Ohi-Toma *et al.* (2010) in the DDBJ and GenBank, were added to the analysis.

PHYLOGENETIC ANALYSES

For each of the plastid regions, nucleotide sequences were manually aligned by considering nucleotide changes and sequence motifs in the non-coding regions. In the matrix for the maximum parsimony (MP) analysis, gap coding was employed using the criteria described in Ohi-Toma *et al.* (2010), and the coded gap states were included as unweighted fifth characters. In the data matrix, when substitutions or overlapping gaps were found in the gap positions among nucleotide sequences, 'n' was added to the position of substitution and/or gap-state to reflect changes. However, length polymorphisms caused by mononucleotide repeats [poly (A) or poly(T)] and portions that could not be aligned due to ambiguities in the alignment were excluded from tree searches.

Phylogenetic relationships were analyzed by MP and the maximum likelihood (ML) methods using PAUP* v.4.0b10 (Swofford, 2002). Because the phylogenetic resolution in preliminary analyses for each of the regions was insufficient, phylogenetic analyses were conducted based on combined sequences of the four regions. In the MP analysis, nucleotide substitutions and coded gaps were used with equal weighting. To search for the shortest trees, the MP analysis was performed using the heuristic search option with simple addition sequences, including tree-bisection-reconnection (TBR) branch swapping, MulTrees in effect and MaxTree limit were set to 100 000. The strict consensus tree from the most parsimonious trees was generated and character changes (substitutions and gaps) were reconstructed on the tree with ACCTRAN character optimization in PAUP*. The MP bootstrap support (BS) values were estimated using a heuristic search with 1000 replicates and simple sequence addition, TBR branch swapping, MulTrees in effect and MaxTree limit set to 100. In the ML analysis, the best model and parameter values for the combined matrix were estimated based on substitutions only using the Akaike information criterion (AIC) in Modeltest v.3.7 (Posada & Crandall, 1998). Heuristic searches were

conducted using the best-fit model (i.e. GTR + I + G) and ten replicates of random sequence addition. An estimation of BS was conducted using a heuristic search with 100 replicates, *as-is* sequence addition, TBR branch swapping and MulTrees in effect.

RESULTS

The sequence lengths of all four plastid regions for 156 ingroup samples varied as follows: 377–437 bp (aligned length 529 bp) for *3'trnL-trnF*; 804–853 bp (aligned length 917 bp) for *rpl20-5'rps12*; 676–710 bp (aligned length 750 bp) for *psbB-psbH*; and 516–549 bp (aligned length 636 bp) for *rpoC2-rps2*. In the data matrix including outgroups, these regions included 42, 71, 59 and 32 potentially parsimony-informative substitution sites, respectively. Nucleotide sequences from the four regions were combined and they formed the final matrix used in the phylogenetic analyses (total aligned length 2858 bp). In addition, 44 coded gaps were added to the data matrix for MP analysis (total length 2902 bp) and the regions included four, seven, five and seven coded gaps that were potentially parsimony informative, respectively. Of the 156 ingroup samples, nucleotide sequences of c. 30 accessions from the Japanese species were identical.

The MP analysis resulted in a strict consensus tree from 100 000 most-parsimonious trees (a limit of MaxTrees) with tree length of 585 (CI = 0.70, RC = 0.64) generated with branch lengths (Fig. 1). In the phylogenetic relationships among the ingroup accessions, which are monophyletic with 100% BS, eight major clades (MP clades I: 56% BS; II: 97% BS; IV: 96% BS; V: 89% BS; VI: 97% BS; VII: 80% BS; VIII: 99% BS; and IX: 80% BS) and one branch with unique sequence variation (*A. fimbriatum* Mast.; i.e. clade III) were detected. The phylogenetic relationships among these clades were unclear due to a polytomy, although clades VII, VIII and IX formed a weakly supported clade (62% BS). Clade IX, containing more than half of the in-group samples, included several internal clades, most of which were not strongly supported.

The ML phylogenetic tree was constructed based on substitutions using the best-fit model (i.e. GTR + I + G), and a single optimal tree with $-\ln L = 7523.51718$ (Fig. 2). Eight major clades in the in-group (ML clades I: 71% BS; II: 95% BS; IV: 91% BS; V: 94% BS; VI: 96% BS; VII: 61%; VIII: 90%; and IX: 77% BS) and one branch with unique sequence variation (*A. fimbriatum*; i.e. clade III) were resolved. Clade III was related to clade IV, and clades V–IX were clustered together, although with weak statistical support (< 50% BS). Clades VII–IX formed a weak clade (61% BS). The largest clade,

clade IX, included internal clades with strong statistical support and unresolved internal clades. The ML optimal tree topology was mostly identical to the MP strict consensus tree (Fig. 1) and members of each clade detected in the ML tree corresponded to those of clades detected in the MP tree.

DISCUSSION

AN UPDATED GENUS-WIDE PHYLOGENETIC TREE FOR *ARISAEMA*

Arisaema contains a wide diversity of species with unique morphological traits and, as a result, numerous taxonomic treatments for its infrageneric classification have been proposed, especially at the sectional level (Table 1). Recently, a comprehensive monograph of the genus, based on morphological characteristics (Gusman & Gusman, 2002, 2006), and the first genus-wide phylogenetic tree (Renner *et al.*, 2004) were published at the same time. Gusman & Gusman (2006), an updated version of Gusman & Gusman (2002), partly accounted for the phylogenetic assessment by Renner *et al.* (2004), but they did not strictly adhere to it in their sectional classification. In contrast, Renner *et al.* (2004) basically followed the sectional classification of Murata (1984, 1991; Table 1), despite discussing the results of Gusman & Gusman (2002). Conversely, Murata (2011) and Murata *et al.* (2013) published a revised sectional classification based on an unpublished, tentative molecular phylogenetic analysis.

In the present study, we provided an updated genus-wide phylogenetic tree of *Arisaema* based on a large data set of four plastid non-coding regions from 138 taxa representing the diversity of the genus. The resultant MP and ML phylogenetic trees (Figs 1, 2, respectively) provided better resolution of the relationships in the genus than the previous phylogenetic tree of Renner *et al.* (2004). Both of our phylogenetic trees identified eight major clades and one branch with unique sequence variations (clades I–IX) which formed a polytomy. The phylogenetic trees did not support the early branching position of *A. tortuosum* detected by Renner *et al.* (2004) because that species was nested in clade I.

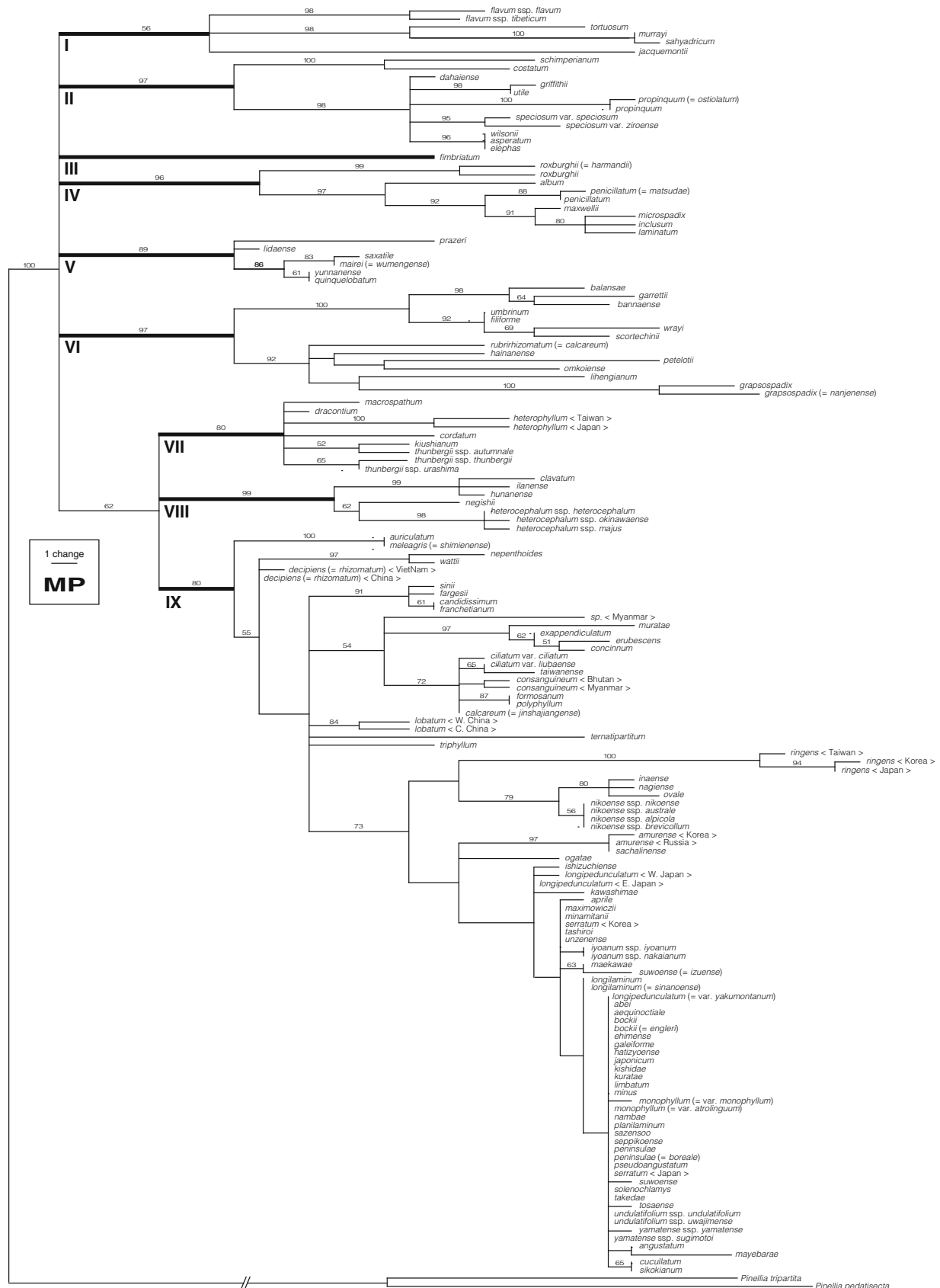
COMPARISON OF INFRAGENERIC CLASSIFICATIONS AND PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships identified here (clades I–IX) are compared with two recent classification systems in Table 1 (Fig. 3). Of the 15 sections proposed by Gusman & Gusman (2006), excluding the monotypic sections and the four small sections consisting of only a few species [*Decipientia* (Engl.) H.Li, *Dochafa* (Schott) H.Hara, *Lobata* Gusman & L.Gusman ex Gusman & L.Gusman and *Tenuipistillata* (Engl.) H.Hara], only two sections formed strongly supported monophyletic groups (> 80% BS): section *Attenuata* (Engl.) H.Li (= clade V) and section *Anomala* (= clade VI). Five sections were polyphyletic [*Tortuosa*, *Sinarisaema*, *Flagellarisaema* (Nakai) H.Hara, *Clavata* and *Nepenthoidea* (Engl.) Gusman & L.Gusman] and members of sections *Tortuosa* and *Clavata* were scattered among several distantly related clades.

In contrast, of the 14 sections in the system of Murata (2011) and Murata *et al.* (2013), seven (*Anomala*, *Clavata*, *Flagellarisaema*, *Franchetiana*, *Odorata*, *Sinarisaema* and *Tortuosa*) were monophyletic, excluding the monotypic section *Dochafa*. Of these seven, four sections corresponded to major clades: *Odorata* (= clade V); *Anomala* (= clade VI); *Flagellarisaema* (= clade VII); and *Clavata* (= clade VIII). Sections *Tortuosa* (in clade I) and *Franchetiana* (in clade IX) were apparently monophyletic, respectively. Section *Sinarisaema* appeared to form a monophyletic group (clade IX), but support for this was weak. Although this sectional system incorporated an unpublished, tentative molecular phylogenetic analysis and a morphological reevaluation, the system still requires taxonomic revision for non-monophyletic sections, owing to the incongruence between the phylogenetic clades and the diagnostic characteristics of each section.

We then reviewed the infrageneric classification of *Arisaema* in the major phylogenetic groups (Table 1 and Fig. 3). To distinguish the sections from the latest system (Murata, 2011; Murata *et al.*, 2013; Table 1), the sections used in other classification systems are indicated with single quotation marks.

Figure 1. Strict consensus tree of the 100 000 (limit of MaxTrees) most parsimonious trees based on the combined sequences of four plastid non-coding regions: 3'*trnL-trnF*, *rpl20–5'rps12*, *psbB-psbH*, and *rpoC2-rps2* (length = 585, CI = 0.70, RC = 0.64). Branch lengths were estimated based on ACCTRAN character optimization and a scale bar (one site change) is shown. Bootstrap support values (> 50%) are shown above the branches. Eight major clades and one branch (thick lines) were designated as clades I–IX. Names of in-groups show only the species epithets. For some species, their synonyms or their identification in Renner *et al.* (2004) are shown in parentheses. For species in which multiple samples were analysed, the locality is shown in angled brackets.



PHYLOGENETIC IMPLICATIONS OF SECTIONS *TORTUOSA*,
TENUPISTILLATA AND *ARISAEMA*

Clade I consisted of species from Indo-Himalayan and adjacent regions and included three sections (Fig. 3): the monotypic *Dochafa* [*A. flavum* (Forssk.) Schott], *Tortuosa* [*A. tortuosum*, *A. murrayi* (J.Graham) Hook. and *A. sahyadricum* S.R.Yadav] and *Tenuipistillata* (*A. jacquemontii* Blume). However, the clade could not be recognized as a single section, because it was not strongly supported and has no morphological synapomorphies.

Although the relationship among the three sections remains unclear, the members of section *Tortuosa* form a monophyletic group in the clade (MP BS 98%; ML BS 97%). Previously, 'section *Tortuosa*' had been widely circumscribed and included species distributed in the Indo-Himalayan, Sino-Japanese and North American regions (Hara, 1971; Murata, 1984; Table 1). However, Gusman & Gusman (2002) separated a few species with a sigmoid spadix appendage ending in a flagellate thread as 'section *Flagellarisaema*'. Then, by considering the phylogenetic relationships identified by Renner *et al.* (2004), Gusman & Gusman (2006) recognized 'section *Attenuata*', which consisted of several species from 'section *Tortuosa* subsection *Attenuata*', *sensu* Gusman & Gusman (2002). In contrast, Murata (2011) moved several species of 'section *Tortuosa*' to section *Clavata* or section *Flagellarisaema* and recognized section *Tortuosa* as a small section of only five Indo-Himalayan species (Table 1).

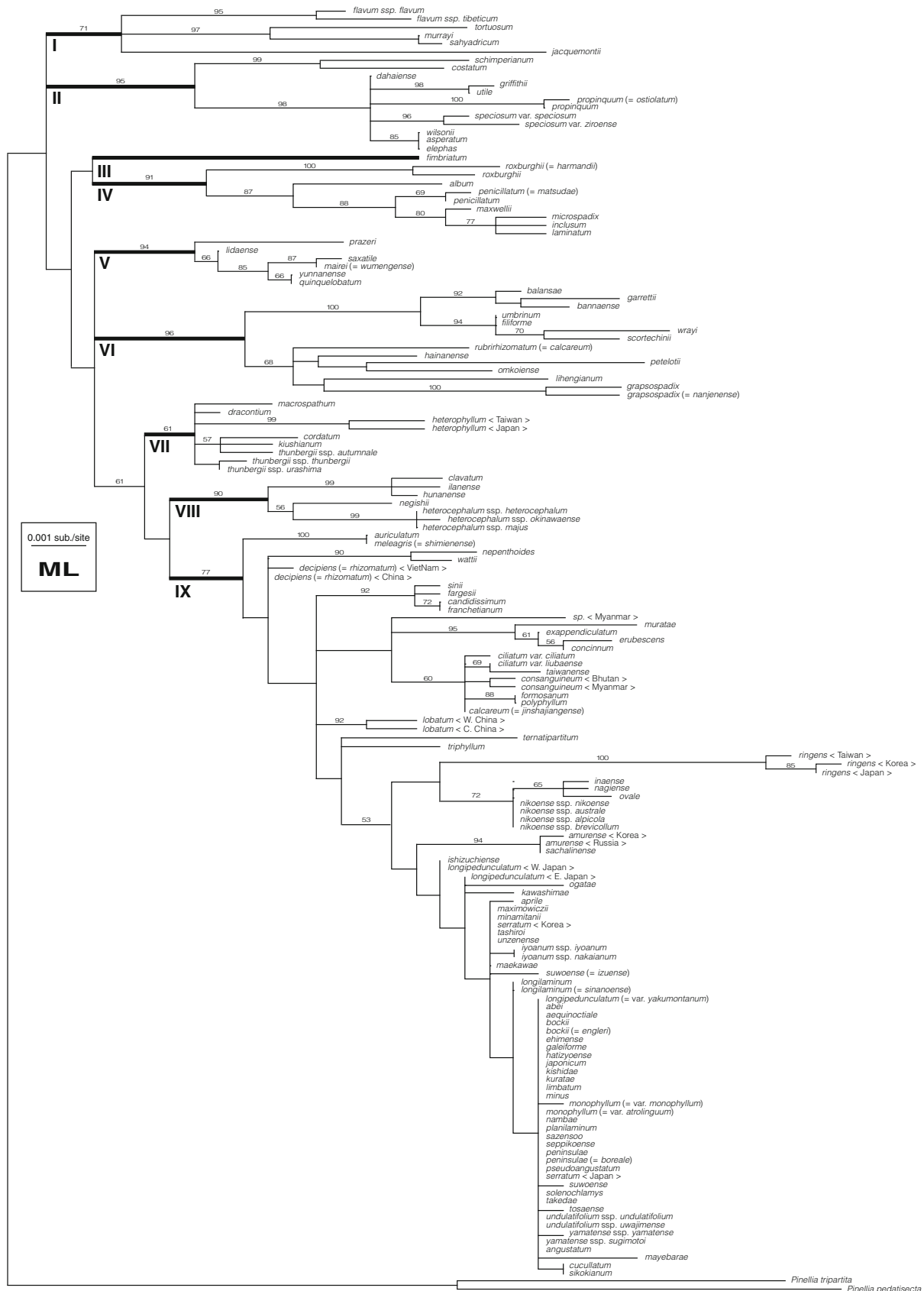
Of the two species in section *Tenuipistillata* that were analysed in the present study, the type species of the section, *A. jacquemontii*, which is distributed in the Indo-Himalayas and China, was included in clade I. However, the other species, *A. schimperianum*, which is in Africa, fell into clade II, corresponding to section *Arisaema*, and was sister to the Himalayan species *A. costatum*. Thus, the relationship between *A. schimperianum* and *A. costatum*, was originally demonstrated by Renner *et al.* (2004), was confirmed by our analysis of newly collected samples. Previously, Renner *et al.* (2004) noted that the quincuncial leaf arrangement of *A. schimperianum* is shared with species of 'section *Arisaema*', including *A. costatum*. Gusman & Gusman (2006) classified *A. schimperianum* in 'section *Sinarisaema*' and recognized 'section *Tenuipistillata*' as a small group that

consisted of only three species from the Indo-Himalayas and China. However, Murata (2011) treated the three species, with nine African species, including *A. schimperianum*, as members of section *Tenuipistillata*, based on their spindle-shaped ovaries. Although the taxonomic treatment of *A. schimperianum* and its African allies has been unstable (e.g. Engler, 1920; Mayo & Gilbert, 1986; Renner *et al.*, 2004; Gusman & Gusman, 2006; Murata, 2011), *A. schimperianum* should be placed in section *Arisaema* rather than section *Tenuipistillata* or 'section *Sinarisaema*'. In their initial analysis of 3'*trnL-trnF* sequences, Renner *et al.* (2004) indicated that another African species with pedate leaves, *A. mildbraedii* Engl., was sister to *A. schimperianum* with radiate leaves and *A. costatum* with trifoliolate leaves. Therefore, the taxonomic status of the other African and Chinese species of section *Tenuipistillata*, which were not available for inclusion in this phylogenetic analysis, should be investigated in future studies.

SEPARATION OF SECTION *FIMBRIATA* FROM SECTION
ATTENUATA

Members of clades III and IV were concordant with the evergreen section *Attenuata*, which is distributed in tropical and subtropical habitats (Fig. 3). Although Gusman & Gusman (2006) treated this group as 'section *Fimbriata*', Murata (2011) synonymised it under section *Attenuata*, in accordance with nomenclatural rules (see also Murata *et al.*, 2013, 2014). Members of section *Attenuata* are readily identified by trifoliolate leaves, solitary axillary buds without accessory buds and a sessile spadix appendage that frequently bears sterile flowers; however, clades III and IV were not strictly monophyletic in the MP and ML phylogenetic trees (Figs 1, 2). Clade III consisted of only a Southeast Asian species, *A. fimbriatum*, and differed significantly from clade IV by unique sequence variation in the phylogenetic trees. In addition, *A. fimbriatum* is morphologically distinct from the other species in clade IV, based on its bisexual spadix and the long spadix appendage that extends from its spathe. Gusman & Gusman (2006) also mentioned that *A. fimbriatum* differed from other species of 'section *Fimbriatum*' on the basis of germination characteristics. Therefore, on

Figure 2. Maximum likelihood tree based on the combined sequences of four plastid non-coding regions: 3'*trnL-trnF*, *rpl20-5'rps12*, *psbB-psbH*, and *rpoC2-rps2* (the best-fit model, GTR + I + G; $-\ln L = 7523.51718$). A scale bar of branches (0.001 substitutions per site) is shown. Bootstrap support values (> 50%) are shown above the branches. Eight major clades and one branch (thick lines) were designated as clades I–IX. Names of in-groups show only the species epithets. For some species, their synonyms or their identification in Renner *et al.* (2004) are shown in parentheses. For species in which multiple samples were analysed, the locality is shown in angled brackets.



the basis of both phylogenetic and morphological evidence, *A. fimbriatum* (= clade III) is treated as an independent group: section *Fimbriata* (Engl.) H.Li (see Taxonomic treatment).

PHYLOGENETIC DISTINCTION OF SECTIONS *ODORATA*, *ANOMALA*, *FLAGELLARISAEMA* AND *CLAVATA*

Two well supported clades, clades V and VI, correspond to the sections *Odorata* and *Anomala*, respectively (Fig. 3). The type species (*A. odoratum* and *A. anomalum*, respectively) could not be included in the present study, but both sections are characterized by distinct morphological traits. Clade V includes species from south-western China and adjacent regions that have sessile, slender, subulate spadix appendages with a recurved or sigmoidally curved apex and trifoliate or pedate leaves. Although Gusman & Gusman (2006) applied 'section *Attenuata*' to this group, Murata *et al.* (2013) legitimately named this group section *Odorata* (Table 1). In contrast, Clade VI corresponds to the evergreen section *Anomala*, which is characterized by an elongated, rhizomatous underground stem with a purplish interior and is distributed throughout tropical and subtropical Asia.

Clades VII, VIII and IX were monophyletic with weak support values and their relationships were unclear, owing to a polytomy (Fig. 3). However, the branching pattern of our phylogenetic tree did not support the monophyly of the sections proposed by Gusman & Gusman (2006), especially for the polyphyletic sections '*Tortuosa*', '*Flagellarisaema*' and '*Clavata*'. Clades VII (with moderate support) and VIII (with strong support) corresponded to sections *Flagellarisaema* and *Clavata*, respectively, *sensu* Murata (2011). These sections share pedate leaves and sessile spadix appendages, but *Clavata* is distinct in having axillary accessory buds and sterile flowers on its spadix appendages.

PHYLOGENETIC RELATIONSHIPS OF OTHER SECTIONS

Clade IX included half of the species in the genus, which were classified into five sections [*Nepenthoidea*, *Decipientia*, *Franchetiana*, *Sinarisaema* and *Pistillata* (Engl.) Nakai]; however, the phylogenetic relationships in the clade remain unclear, owing to weak branch support (Figs 1, 2).

Section *Nepenthoidea* did not form a clade (Fig. 3), because *A. auriculatum* Buchet and *A. meleagris* Buchet were not closely related to *A. nepenthoides* (Wall.) Mart. ex Schott, which is the type species of the section. Due to its unique morphology, *A. auriculatum* was placed in 'section *Flagellarisaema*' by Gusman & Gusman (2006), but this treatment was not supported by phylogenetic analyses. In contrast,

Murata (2011) provisionally placed *A. auriculatum* in section *Nepenthoidea* by considering an unpublished, tentative phylogenetic analysis. Furthermore, *A. auriculatum* and *A. meleagris* are morphologically similar (Li *et al.*, 2010) and distinct from *A. nepenthoides* and *A. wattii* Hook.f. in having a stoloniferous tuber. However, the four species share a brownish, olive-green spathe, mottled with pink, purple and brown, that opens earlier than the leaves. Therefore, the species relationships in section *Nepenthoidea* should be further discussed on the basis of a highly resolved phylogenetic assessment.

Section *Decipientia* is distinguished by a rhizomatous tuber rooting all over and autumn flowering. Gusman & Gusman (2006) suggested that 'section *Decipientia*' resembled section *Nepenthoidea*, based on morphological traits, such as its quincuncial phyllotaxy and a short, stipitate spadix appendage without sterile flowers. In the phylogenetic tree, two accessions of *A. decipiens* Schott were located near the branch of *A. nepenthoides* and *A. wattii* (Figs 1 and 2), but the relationship between sections *Decipientia* and *Nepenthoidea* is unclear.

In clade XI, one well supported internal clade corresponded to section *Franchetiana*, which consists of species with trifoliate leaves from western China and adjacent regions. In section *Franchetiana*, *A. sinii* K.Krause, classified in 'section *Clavata*' by Gusman & Gusman (2006), was morphologically different from the other members of the section, in having sterile flowers above fertile flowers on its sessile spadix appendage.

Species of section *Sinarisaema* are characterized by spirodistichous phyllotaxis and most have radially arranged leaflets. In the phylogenetic tree, the clade that included the species of *Sinarisaema* was not strongly supported. However, the branching pattern indicated that *A. calcareum* H.Li, which has trifoliate leaves, was closely related to several species of *Sinarisaema* (Fig. 3), in contrast with its previous placement in 'section *Clavata*' (Gusman & Gusman, 2006) or 'section *Fimbriata*' (Li *et al.*, 2010). In section *Sinarisaema*, a species group consisting of *A. erubescens* (Wall.) Schott, *A. consanguineum* Schott and *A. formosanum* Hayata was recently treated as a single species, *A. erubescens* (Li *et al.*, 2010). However, considering their phylogenetic differences and certain morphological traits (Gusman & Gusman, 2006), *A. consanguineum* and *A. formosanum* should be treated as distinct from *A. erubescens*. Incidentally, one unknown plant from Myanmar, which is similar to *A. concinnum* Schott in having radiate leaves and a slender spadix surrounded by a green spathe with longitudinal white stripes, exhibited unique sequence variations ('sp.' in Figs 1 and 2) and may represent a new species.

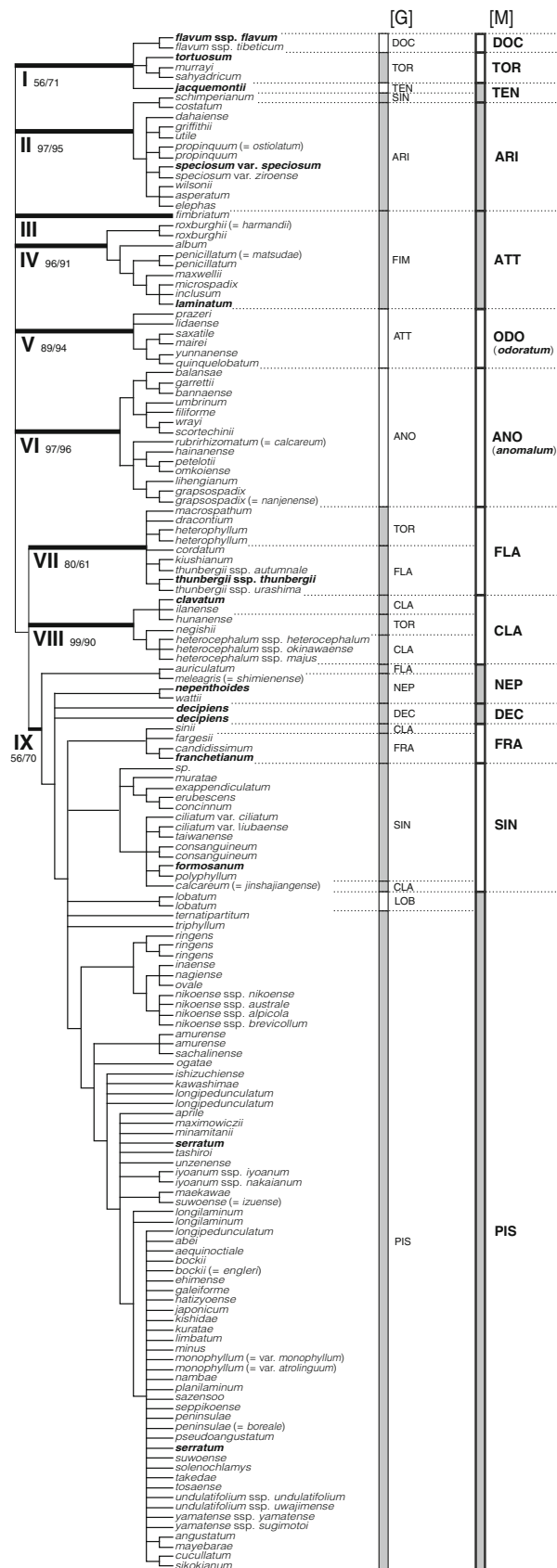


Figure 3. Summary of the phylogenetic relationship of *Arisaema* and two recent classifications from Table 1: [G] Gusman & Gusman (2006); [M] Murata (2011) and Murata *et al.* (2013). The phylogenetic tree depicts the branching pattern without branch lengths (clades with bootstrap support values from MP/ML analyses) in the strict consensus tree of MP trees. Sections in each classification system are represented on the right side of the tree and the names of sections are shown as abbreviations: ANO, *Anomala*; ARI, *Arisaema*; ATT, *Attenuata*; CLA, *Clavata*; DEC, *Decipiens*; DOC, *Dochafa*; FIM, *Fimbriata*; FLA, *Flagellarisaema*; FRA, *Franchetiana*; NEP, *Nepenthoidea*; ODO, *Odorata*; PIS, *Pistillata*; SIN, *Sinarisaema*; TEN, *Tenuipistillata*; and TOR, *Tortuosa*. Sections in Murata (2011) and Murata *et al.* (2013) are indicated in bold and the type species of each section is indicated in bold. Monophyletic and non-monophyletic sections are indicated by white and grey bars, respectively.

Murata (2011) classified 50 species and six subspecies in section *Pistillata* (from *A. lobatum* to *A. sikokianum* in clade IX; Fig. 3). Most of the species have pedate leaves, although a few species have trifoliolate leaves and have previously been distinguished as a distinct genus or a distinct section (Table 1); i.e. *A. lobatum* Engl. ('section *Lobata*'), *A. ringens* (Thunb.) Schott [genus *Ringentiarum* Nakai or 'section *Pistillata* subsection *Ringentia* (Engl.) G. & L. Gusman'], and *A. ternatipartitum* Makino ('section *Colocasiarum* Nakai'). Recently, Murata (2011) characterized section *Pistillata* with an emphasis on spirodistichous phyllotaxis. It is notable that most species of this section, except six species, are endemic to Japan. They also exhibit remarkable morphological diversity, even though a large number of species shared identical nucleotide sequences (Figs 1, 2). Previously, extremely low genetic differentiation among Japanese species was reported, based on allozyme variation (Murata & Kawahara, 1997). Thus, low genetic diversity in section *Pistillata* suggests that a morphological radiation recently occurred in a narrow region of the Japanese archipelago.

TAXONOMIC TREATMENT

Based on morphological characters and phylogenetic relationships, we recognize 15 sections in *Arisaema*, adding an additional section to the 14 sections recognized by Murata (2011) and Murata *et al.* (2013).

Arisaema section *Fimbriata* (Engl.) H. Li in Fl. Reipubl. Popul. Sin. 13: 123. 1979, p.p. ≡ *A.* [unranked] *Fimbriata* Engl. in Pflanzenr. (Engler) IV 23F (Herft 73): 151. 1920. – Type: *A. fimbriatum* Mast., Gard. Chron., n.s. 22: 680. 1884.

Note: section *Fimbriata* has been recognized since Li (1979) published it as the section comprising six

species based on Engler (1920)'s unranked *Fimbriata*, but it was synonymised under section *Attenuata* by Murata (2011; Table 1) Here, the section is redefined as a monotypic section, which is characterized by a bisexual spadix and a long spadix appendage that extends from the spathe.

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Appendix

List of accessions used in the present study, indicating the species, source, voucher information and DDBJ/GenBank accession numbers of the four plastid non-coding regions (i.e. 3'*trnL-trnF*, *rpl20-5'rp-s12*, *psbB-psbH*, and *rpoC2-rps2*). Accessions are listed according to the sectional classification proposed in the present study. The identification of some of the samples used by Renner *et al.* (2004) is revised, according to recent treatments, and is quoted in parentheses following the species name. Some species recognized by Gusman & Gusman (2006), which have more recently been treated as synonyms, are quoted in parentheses. Names of several gardens that cultivated samples are shown as abbreviations: KEW (Royal Botanic Gardens, Kew, UK), KBG (Koishikawa Botanical Gardens, The University of Tokyo, Japan), NBG (Nikko Botanical Gardens, The University of Tokyo, Japan) and MGSU (Medicinal Garden of Setsunan University, Japan). Asterisks (*) indicate DDBJ/GenBank accession numbers obtained from Ohi-Toma *et al.* (2010). Accessions with a superscript figure (¹) following the voucher specimen were used by Renner *et al.* (2004).

Arisaema Mart. section **Anomala** Gusman & L.Gusman – **A. balansae** Engl.: Vietnam, Son La, Harder *et al.* 5739 (MO)¹, AB982303, AB982458, AB982613, AB982768; **A. bannaense** H.Li: China, Yunnan, Murata Arisa136 (TI), AB982347, AB982502, AB982657, AB982812; **A. filiforme** (Reinw.) Blume: Indonesia, Java (cult. in NBG), Murata 27003 (TI), AB982362, AB982517, AB982672, AB982827; **A. garrettii** Gagnep.: Thailand, Chiang Rai, Gusman 00012 (MO)¹, AB982315, AB982470, AB982625, AB982780; **A. grapsospadix** Hayata: Taiwan, Nantou, Ohi-Toma & Watanabe-Toma Arisa236 (TI), AB982366, AB982521, AB982676, AB982831; **A. grapsospadix** (= *A. nanjenense* T.C.Huang & M.J.Wu): Taiwan, Pingtung (cult. in KBG), Murata Arisa007 (TI), AB982367, AB982522, AB982677, AB982832; **A. hainanense** C.Y.Wu ex H.Li, Y.Shiao & S.L.Tseng: China, Hainan, Murata *et al.* Arisa234 (TI), AB982368, AB982523, AB982678, AB982833; **A. lihengianum** J.Murata & S.K.Wu: China, Yunnan, Murata

Arise030 (TI), AB982387, AB982542, AB982697, AB982852; **A. omkoiense** Gusman: Thailand (cult. in KBG), Murata 27004 (TI), AB982414, AB982569, AB982724, AB982879; **A. petelotii** K.Krause: Vietnam, Son La, Harder *et al.* 5824 (MO)¹, AB982329, AB982484, AB982639, AB982794; **A. rubrirhizomatium** H.Li & J.Murata [= *A. calcareum* H.Li in Renner *et al.* (2004)]: China, Bruggerman s.n. (MO)¹, AB982304, AB982459, AB982614, AB982769; **A. scortechinii** Hook.f.: Malaysia (cult. in MGSU), Murata Arisa025 (TI), AB982431, AB982586, AB982741, AB982896; **A. umbrinum** Ridl.: Malaysia, Sarawak, Hettterscheid H.AR47 (MO)¹, AB982335, AB982490, AB982645, AB982800; **A. wrayi** Hemsl.: Malaysia, Perak, Gusman 99005 (MO)¹, AB982338, AB982493, AB982648, AB982803. **Ariseaema** section **Ariseaema** – **A. asperatum** N.E.Br.: cult. in MGSU, Murata Arisa071 (TI), AB982345, AB982500, AB982655, AB982810; **A. dahaiense** H.Li: Myanmar, Mt.Victoria, Tanaka *et al.* 030552 (MBK), AB982355, AB982510, AB982665, AB982820; **A. costatum** (Wall.) Mart. ex Schott: Nepal (cult. in KBG), Murata Arisa248 (TI), AB982353, AB982508, AB982663, AB982818; **A. elephas** Buchet: cult. in MGSU, Murata Arisa073 (TI), AB982360, AB982515, AB982670, AB982825; **A. griffithii** Schott: Nepal, Gusman 97013 (MO)¹, AB982316, AB982471, AB982626, AB982781; **A. propinquum** Schott: India, West Bengal, Bruggerman s.n. (MO)¹, AB982330, AB982485, AB982640, AB982795; **A. propinquum** [= *A. ostiolatum* H.Hara in Renner *et al.* (2004)]: India, West Bengal, Bruggerman 015 (MO)¹, AB982327, AB982482, AB982637, AB982792; **A. schimperianum** Schott: Ethiopia (cult. in KBG), Murata Arisa023 (TI), AB982430, AB982585, AB982740, AB982895; **A. speciosum** (Wall.) Mart. ex Schott var. **speciosum**: cult., Hettterscheid H.AR.294 (MO)¹, AB982643, AB982333, AB982488, AB982798; **A. speciosum** var. **zironense** Gusman: India, Arunachal, Gusman 97143 (MO)¹, AB982334, AB982489, AB982644, AB982799; **A. utile** Hook.f. ex Schott: cult., Hettterscheid s.n. (MO)¹, AB982336, AB982491, AB982646, AB982801; **A. wilsonii** Engl.: China, Sichuan, Gusman 92103 (MO)¹, AB982337, AB982492, AB982647, AB982802. **Ariseaema** section **Attenuata** (Engl.) H.Li – **A. album** N.E.Br.: India, Meghalaya, Gusman 97147 (MO)¹, AB982302, AB982457, AB982612 AB982767; **A. inclusum** (N.E.Br.) N.E.Br. ex B.D.Jacks.: Indonesia, Java (cult. in NBG), Murata MS001 (TI), AB982376, AB982531, AB982686, AB982841; **A. laminatum** Blume: Indonesia, South Kalimantan, Murata Arisa028 (TI), AB982385, AB982540, AB982695, AB982850; **A. maxwellii** Hett. & Gusman: Thailand (cult. in MGSU), Murata *et al.*

Arisa020 (TI), AB982399, AB982554, AB982709, AB982864; **A. microspadix** Engl.: Indonesia, Bali, *Murata* 25-21 (TI)¹, AB982324, AB982479, AB982634, AB982789; **A. penicillatum** N.E.Br.: China, Hong Kong, *Gusman* 01048 (MO)¹, AB982328, AB982483, AB982638, AB982793; **A. penicillatum** [= *A. matsudae* Hayata in Renner et al. (2004)]: Taiwan, Kaohsiung, *Chang* 5117 (TNU)¹, AB982323, AB982478, AB982633, AB982788; **A. roxburghii** Kunth: Thailand, *Murata Arisa241* (TI), AB982426, AB982581, AB982736, AB982891; **A. roxburghii** [= *A. harmandii* Engl. in Renner et al. (2004)], Thailand, Nam Nao, *Hettterscheid* H.AR.220 (MO)¹, AB982317, AB982472, AB982627, AB982782. **Arisaema** section **Clavata** (Engl.) H.Ohashi & J.Murata – **A. clavatum** Buchet: China, Sichuan, *Murata et al. Arisa212* (TI), AB982349, AB982504, AB982659, AB982814; **A. heterocephalum** Koidz. subsp. **heterocephalum**: Japan, Kagoshima, *Kobayashi* 42836 (TI), AB982370, AB982525, AB982680, AB982835; **A. heterocephalum** subsp. **majus** (Seriz.) J.Murata: Japan, Kagoshima, *Kobayashi* 42835 (TI), AB982371, AB982526, AB982681, AB982836; **A. heterocephalum** subsp. **okinawaense** H.Ohashi & J.Murata: Japan, Okinawa, *Murata Arisa140* (TI), AB982372, AB982527, AB982682, AB982837; **A. hunanense** Hand.-Mazz.: China, *Bruggeman s.n.* (MO)¹, AB982318, AB982473, AB982628, AB982783; **A. ilanense** J.C.Wang: Taiwan, Ilan, *Wang* 11620 (TNU)¹, AB982319, AB982474, AB982629, AB982784; **A. negishii** Makino: Japan (cult. in KBG), *Ohi-Toma Arisa027* (TI), AB982408, AB982563, AB982718, AB982873. **Arisaema** section **Decipientia** (Engl.) H.Li – **A. decipiens** Schott (= *A. rhizomatum* C.E.C.Fisch.): Vietnam, Sapa, *Murata & Ohi-Toma Arisa134* (TI), AB982356, AB982511, AB982666, AB982821; **A. decipiens** (= *A. rhizomatum*): China, Yunnan, *Murata et al. Arisa238* (TI), AB982357, AB982512, AB982667, AB982822. **Arisaema** section **Dochafa** (Schott) H.Hara – **A. flavum** (Forssk.) Schott subsp. **flavum**: Afghanistan (cult. in KEW), *Murata Kew68430* (K)¹, AB982313, AB982468, AB982623, AB982778; **A. flavum** subsp. **tibeticum** (J.Murata) Gusman & L.Gusman: China, Tibet, *Chambers s.n.* (MO)¹, AB982314, AB982469, AB982624, AB982779. **Arisaema** section **Fimbriata** (Engl.) H.Li – **A. fimbriatum** Mast.: Malaysia, Langkawi Island, *Gusman* 01098 (MO)¹, AB982312, AB982467, AB982622, AB982777; **Arisaema** section **Flagellarisaema** (Nakai) H.Hara – **A. cordatum** N.E.Br.: China, Hong Kong, *Gusman* 01049 (MO)¹, AB982308, AB982463, AB982618, AB982773; **A. dracunculium** (L.) Schott: USA (cult. in KBG), *Murata Arisa005* (TI), AB982358, AB982513, AB982668, AB982823; **A. heterophyllum** Blume: Taiwan (cult.

in KBG), $2n = 28$, *Ohi-Toma Arisa022* (TI), AB982373, AB982528, AB982683, AB982838; **A. heterophyllum**: Japan (cult. in KBG), $2n = 168$, *Ohi-Toma Arisa125* (TI), AB982374, AB982529, AB982684, AB982839; **A. kiushianum** Makino: Japan (cult. in MGSU), *Murata Arisa069* (TI), AB982383, AB982538, AB982693, AB982848; **A. macrospathum** Benth.: Mexico, Michoacan, *Gusman* 97229 (MO)¹, AB982322, AB982477, AB982632, AB982787; **A. thunbergii** Blume subsp. **thunbergii**: Japan, Kagoshima, *Tsukaya Arisa002* (TI), AB982443, AB982598, AB982753, AB982908; **A. thunbergii** subsp. **autumnale** J.C.Wang: J.Murata & H.Ohashi: Taiwan, Ilan, *Watanabe et al. Arisa133* (TI), AB982444, AB982599, AB982754, AB982909; **A. thunbergii** subsp. **urashima** (H.Hara) H.Ohashi & J.Murata: Japan (cult. in KBG), *Ohi-Toma Arisa003* (TI), AB982445, AB982600, AB982755, AB982910. **Arisaema** section **Franchetiana** (Engl.) H.Hara – **A. candidissimum** W.W.Sm.: cult., *Hettterscheid s.n.* (MO)¹, AB982305, AB982460, AB982615, AB982770; **A. fargesii** Buchet: cult. in KEW (67447), *Murata Arisa075*, AB982361, AB982516, AB982671, AB982826; **A. franchetianum** Engl.: cult. in KBG, *Murata Arisa006* (TI), AB982364, AB982519, AB982674, AB982829; **A. sinii** K.Krause: China, Yunnan, *Murata Arisa228* (TI), AB982435, AB982590, AB982745, AB982900. **Arisaema** section **Nepenthoidea** (Engl.) Gusman & L.Gusman – **A. auriculatum** Buchet: China, Sichuan, *Murata Arisa211* (TI), AB982346, AB982501, AB982656, AB982811; **A. meleagris** Buchet [= *A. shimienense* H.Li in Renner et al. (2004)]: China, *Bruggeman s.n.* (MO)¹, AB982332, AB982487, AB982642, AB982797; **A. nepenthoides** (Wall.) Mart. ex Schott: cult., *Magrys s.n.* (MO)¹, AB982326, AB982481, AB982636, AB982791; **A. wattii** Hook.f., Myanmar, Mt. Victoria, *Tanaka et al. 030579* (MBK), AB982452, AB982607, AB982762, AB982917. **Arisaema** section **Odorata** J.Murata – **A. lidaense** J.Murata & S.K.Wu: China, Yunnan, *Akiyama et al. 078* (TI), AB982386, AB982541, AB982696, AB982851; **A. mairei** H.Lév.: cult. in NBG, *Murata Arisa092* (TI), AB982397, AB982552, AB982707, AB982862; **A. prazeri** Hook.f.: Myanmar, *Murata Arisa026* (TI), AB982420, AB982575, AB982730, AB982885; **A. saxatile** Buchet: cult., *Chapman s.n.* (MO)¹, AB982331, AB982486, AB982641, AB982796; **A. yunnanense** Buchet: China, Yunnan, *Murata et al. Arisa091* (TI), AB982455, AB982610, AB982765, AB982920; **A. quinquelobatum** H.Li & J.Murata: China, Yunnan, *Murata et al. Arisa124* (TI), AB982422, AB982577, AB982732, AB982887. **Arisaema** section **Pistillata** (Engl.) Nakai – **A. abei** Seriz.: Japan, Tokushima, *Kakishima Arisa213* (TI), AB982339, AB982494, AB982649, AB982804; **A. aequinoctiale** Nakai &

- F.Maek.: Japan, Chiba, *Murata Arisa231* (TI), AB982340, AB982495, AB982650, AB982805; **A. amurense** Maxim.: Korea, *Im Arisa188* (TI), AB982342, AB982497, AB982652, AB982807; **A. amurense**: Russia (cult. in KBG), *Ohi-Toma Arisa043* (TI), AB982341, AB982496, AB982651, AB982806; **A. angustatum** Franch. & Sav.: Japan, Shizuoka, *Ohi-Toma Arisa039* (TI), AB982343, AB982498, AB982653, AB982808; **A. aprile** J.Murata: Japan, Shizuoka, *Ohi-Toma Arisa037* (TI), AB982344, AB982499, AB982654, AB982809; **A. bockii** Engl.: China, Zhejiang, *Murata et al. Arisa240* (TI), AB982348, AB982503, AB982658, AB982813; **A. bockii** [= *A. engleri* Pamp. in Renner *et al.* (2004)]: China, *Gusman 98173* (MO)¹, AB982309, AB982464, AB982619, AB982774; **A. cucullatum** M.Hotta: Japan, Nara, *Kobayashi 39256* (TI), AB982354, AB982509, AB982664, AB982819; **A. ehimense** J.Murata & J.Ohno: Japan, Ehime, *Ohi-Toma Arisa232* (TI), AB982359, AB982514, AB982669, AB982824; **A. galeiforme** Seriz.: Japan, Gunma, *Yoshii Arisa111* (TI), AB982365, AB982520, AB982675, AB982830; **A. hatizyoense** Nakai: Japan, Tokyo, *Ohi-Toma Arisa059*, AB982369, AB982524, AB982679, AB982834; **A. inaense** (Seriz.) Seriz. ex K.Sasam. & J.Murata: Japan, Nagano, *Takashima Arisa159* (TI), AB982375, AB982530, AB982685, AB982840; **A. ishizuchiense** Murata: Japan, Tokushima, *Kakishima Arisa190* (TI), AB982377, AB982532, AB982687, AB982842; **A. iyoanum** Makino subsp. *iyoanum*: Japan, Ehime (cult. in KBG), *Ohi-Toma Arisa068* (TI), AB982378, AB982533, AB982688, AB982843; **A. iyoanum** subsp. *nakaianum* (Kitag. & Ohba) H.Obashi & J.Murata: Japan, Ehime, *Kakishima Arisa201* (TI), AB982379, AB982534, AB982689, AB982844; **A. japonicum** Blume: Japan, Tokushima, *Ohi-Toma Arisa013* (TI), AB982380, AB982535, AB982690, AB982845; **A. kawashimae** Seriz.: Japan, Kagoshima, *Kobayashi s.n.* (TI), AB982381, AB982536, AB982691, AB982846; **A. kishidae** Makino ex Nakai: Japan, Wakayama, *Ohi-Toma Arisa249* (TI), AB982382, AB982537, AB982692, AB982847; **A. kuratae** Seriz.: Japan, Shizuoka, *Ohi-Toma Arisa042* (TI), AB982384, AB982539, AB982694, AB982849; **A. limbatum** Nakai & F.Maek.: Japan, Tokyo, *Ohi-Toma Arisa032* (TI), AB982388, AB982543, AB982698, AB982853; **A. lobatum** Engl.: China, Yunnan, *Murata et al. Arisa210* (TI), AB982389, AB982544, AB982699, AB982854; **A. lobatum**: China, Hubei, *Murata et al. Arisa244* (TI), AB982390, AB982545, AB982700, AB982855; **A. longilaminum** Nakai: Japan, Nara, *Yamaguchi & Ohi-Toma Y186*, AB982391, AB982546, AB982701, AB982856; **A. longilaminum** Nakai (= *A. sinanoense* Nakai): Japan, Nagano, *Yamaguchi Y148*, AB982392, AB982547, AB982702, AB982857; **A. longipedunculatum** M.Hotta: Japan, Shizuoka, *Watanabe Arisa127* (TI), AB982393, AB982548, AB982703, AB982858; **A. longipedunculatum**: Japan, Tokushima, *Kakishima Arisa191* (TI), AB982394, AB982549, AB982704, AB982859; **A. longipedunculatum** (= *A. longipedunculatum* var. *yakumontanum* Seriz.): Japan, Kagoshima, *Ohi-Toma Arisa242* (TI), AB982395, AB982550, AB982705, AB982860; **A. maekawae** J.Murata & S.Kakish.: Japan, Yamanashi, *Kakishima Arisa230* (TI), AB982396, AB982551, AB982706, AB982861; **A. mayebarae** Nakai: Japan, Kumamoto, *Ohno Arisa168* (TI), AB982400, AB982555, AB982710, AB982865; **A. maximowiczii** (Engl.) Nakai: Japan, Saga, *Watanabe Arisa090* (TI), AB982398, AB982553, AB982708, AB982863; **A. minamitanii** Seriz.: Japan, Miyazaki, *Minamitani & Takashima Arisa186* (TI), AB982401, AB982556, AB982711, AB982866; **A. minus** (Seriz.) J.Murata: Japan, Hyogo, *Kobayashi 39260* (TI), AB982402, AB982557, AB982712, AB982867; **A. monophyllum** Nakai: Japan, Gunma, *Yoshii Arisa096* (TI), AB982403, AB982558, AB982713, AB982868; **A. monophyllum** [= *A. monophyllum* var. *atrolinguum* (F.Maek.) Kurata]: Japan, Gunma, *Yoshii Arisa099* (TI), AB982404, AB982559, AB982714, AB982869; **A. nagiense** Tom.Kobay., K.Sasam. & J.Murata: Japan, Okayama, *Sasamura et al. SK532* (TI), AB982406, AB982561, AB982716, AB982871; **A. nambae** Kitam.: Japan, Okayama, *Kobayashi 39261* (TI), AB982407, AB982562, AB982717, AB982872; **A. nikoense** Nakai subsp. *nikoense*: Japan, Gunma, *Yoshii Arisa110* (TI), AB982409, AB982564, AB982719, AB982874; **A. nikoense** subsp. *alpicola* (Seriz.) J.Murata: Japan, Fukui, *Wakasugi Arisa081* (TI), AB982410, AB982565, AB982720, AB982875; **A. nikoense** subsp. *australe* (M.Hotta) Seriz.: Japan, Nara, *Kobayashi 39258* (TI), AB982411, AB982566, AB982721, AB982876; **A. nikoense** subsp. *brevicolum* (H.Obashi & J.Murata) J.Murata: Japan, Gifu, *Kobayashi 39257* (TI), AB982412, AB982567, AB982722, AB982877; **A. ogatae** Koidz.: Japan, Miyazaki, *Minamitani & Takashima Arisa187* (TI), AB982413, AB982568, AB982723, AB982878; **A. ovale** Nakai: Japan, Tochigi, *Murata Arisa144* (TI), AB982415, AB982570, AB982725, AB982880; **A. peninsulae** Nakai: Japan, Shiga, *Ohi-Toma Arisa050* (TI), AB982416, AB982571, AB982726, AB982881; **A. peninsulae** Nakai (= *A. boreale* Nakai): Japan, Gifu, *Ohi-Toma Arisa046* (TI), AB982417, AB982572, AB982727, AB982882; **A. planilaminum** J.Murata: Japan, Gunma, *Yoshii Arisa093* (TI), AB982418, AB982573, AB982728, AB982883; **A. pseudoangustatum** Seriz.: Japan, Nagano, *Takashima Arisa184* (TI), AB982421,

AB982576, AB982731, AB982886; **A. ringens** (Thunb.) Schott: Korea, Cheju, *Murata Arisa024* (TI), AB982423, AB982578, AB982733, AB982888; **A. ringens**: Taiwan (cult. in KBG), *Murata Arisa137* (TI), AB982424, AB982579, AB982734, AB982889; **A. ringens**: Japan, Kagoshima, *Ohi-Toma Arisa160* (TI), AB982425, AB982580, AB982735, AB982890; **A. sachalinense** (Miyabe & Kudo) J.Murata: Japan, Hokkaido, *Kawahara Arisa166* (TI), AB982427, AB982582, AB982737, AB982892; **A. sazensoo** (Blume) Makino: Japan, Miyazaki, *Ohi-Toma Arisa162* (TI), AB982429, AB982584, AB982739, AB982894; **A. seppikoense** Kitam.: Japan, Hyogo, *Kobayashi 39259* (TI), AB982432, AB982587, AB982742, AB982897; **A. serratum** (Thunb.) Schott: Japan, Chiba, *Ohi-Toma Arisa222* (TI), AB494509*, AB494543*, AB494577*, AB494645*; **A. serratum**: Korea, Cheju, *Murata et al. Arisa226* (TI), AB982433, AB982588, AB982743, AB982898; **A. sikokianum** Franch. & Sav.: Japan (cult. in MGSU), *Murata Arisa054* (TI), AB982434, AB982589, AB982744, AB982899; **A. solenochlamys** Nakai ex F.Maek.: Japan, Gunma, *Yoshii Arisa112* (TI), AB982436, AB982591, AB982746, AB982901; **A. suwoense** Nakai: Japan, Yamaguchi, *Murata Arisa036* (TI), AB982437, AB982592, AB982747, AB982902; **A. suwoense** (= *A. izuense* Nakai): Japan, Shizuoka, *Ohi-Toma Arisa040* (TI), AB982438, AB982593, AB982748, AB982903; **A. takedae** Makino: Japan, Aichi, *Ohi-Toma Arisa045* (TI), AB982440, AB982595, AB982750, AB982905; **A. tashiroi** Kitam.: Japan, Miyazaki, *Ohi-Toma Arisa161* (TI), AB982441, AB982596, AB982751, AB982906; **A. ternatipartitum** Makino: Japan, Saga, *Watanabe Arisa123* (TI), AB982442, AB982597, AB982752, AB982907; **A. tosaense** Makino: Japan, Tokushima, *Ohi-Toma Arisa219* (TI), AB982447, AB982602, AB982757, AB982912; **A. triphyllum** (L.) Torr.: USA (cult. in KBG), *Murata Arisa157* (TI), AB982448, AB982603, AB982758, AB982913; **A. undulatifolium** Nakai subsp. **undulatifolium**: Japan, Shizuoka, *Ohi-Toma Arisa038* (TI), AB982449, AB982604, AB982759, AB982914; **A. undulatifolium** Nakai subsp. **uwajimense** Tom.-Kobay. & J.Murata: Japan, Ehime, *Ohi-Toma Arisa233* (TI), AB982450, AB982605, AB982760, AB982915; **A. unzenense** Seriz.: Japan, Nagasaki, *Ohi-Toma Arisa239* (TI), AB982451, AB982606, AB982761, AB982916. **A. yamatense** (Nakai) Nakai subsp. **yamatense**: Japan, Nara, *Yoshii Arisa082* (TI), AB982453, AB982608, AB982763, AB982918; **A. yamatense** subsp. **sugimotoi** (Nakai) H. Ohashi &

J.Murata: Japan, Aichi, *Tsukaya Arisa014* (TI), AB982454, AB982609, AB982764, AB982919. **Arisaema** section **Sinarisaema** Nakai – **A. ciliatum** H.Li var. **ciliatum**: China, Yunnan, *Gusman 92118a* (MO)¹, AB982306, AB982461, AB982616, AB982771. **A. ciliatum** H.Li var. **liubaense** Gusman & Gouda: China, Yunnan, *Hettterscheid s.n.* (MO)¹, AB982307, AB982462, AB982617, AB982772; **A. calcareum** H.Li [= *A. jinshajiangense* H.Li in Renner et al. (2004)]: China, Yunnan, *Gusman 00152* (MO)¹, AB982321, AB982476, AB982631, AB982786; **A. concinnum** Schott: Nepal (cult. in NBG), *Tateishi 7927* (TI), AB982350, AB982505, AB982660, AB982815; **A. consanguineum** Schott: Bhutan (cult. in MGSU), *Murata Arisa076* (TI), AB982351, AB982506, AB982661, AB982816; **A. consanguineum**: Myanmar, Mt. Victoria, *Tanaka et al. 030817* (TI), AB982352, AB982507, AB982662, AB982817; **A. erubescens** (Wall.) Schott: Nepal, *Gusman 99007* (MO)¹, AB982310, AB982465, AB982620, AB982775; **A. exappendiculatum** H.Hara: cult., *Hettterscheid H.AR.304* (MO)¹, AB982311, AB982466, AB982621, AB982776; **A. formosanum** Hayata: Taiwan, Nanto, *Ohi-Toma & Watanabe-Toma Arisa235* (TI), AB982363, AB982518, AB982673, AB982828; **A. muratae** Gusman & J.T.Yin: China (cult. in KBG), *Ohi-Toma Arisa246* (TI), AB982405, AB982560, AB982715, AB982870; **A. polyphyllum** (Blanco) Merr.: Philippines (cult. in KBG), *Murata Arisa008* (TI), AB982419, AB982574, AB982729, AB982884; **A. taiwanense** J.Murata: Taiwan, Nanto, *Ohi-Toma & Watanabe-Toma Arisa237* (TI), AB982439, AB982594, AB982749, AB982904; **Arisaema** sp.: Myanmar, *Tanaka et al. 030869* (TI), AB982456, AB982611, AB982766, AB982921; **Arisaema** section **Tenuipistillata** (Engl.) H.Hara – **A. jacquemontii** Blume: India, Himachal, *Gusman 96151* (MO)¹, AB982320, AB982475, AB982630, AB982785. **Arisaema** section **Tortuosa** (Engl.) Nakai – **A. murrayi** (J.Graham) Hook.: India, Maharashtra, *Murata 29* (MO)¹, AB982325, AB982480, AB982635, AB982790; **A. sahyadricum** S.R.Yadav: India (cult. in KBG), *Murata Arisa010* (TI), AB982428, AB982583, AB982738, AB982893; **A. tortuosum** (Wall.) Schott: Bhutan (cult. in NBG), *Murata Arisa077* (TI), AB982446, AB982601, AB982756, AB982911. **Pinellia** Ten. – **P. pedatisecta** Schott: cult. in KBG, *Ohi-Toma Pin01* (TI), AB494510*, AB494544*, AB494578*, AB494646*; **P. tripartita** (Blume) Schott: cult. in KBG, *Ohi-Toma Pin02* (TI), AB494511*, AB494545*, AB494579*, AB494647*.