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Molecular Phylogeny of *Typhonium* sensu lato and Its Allied Genera in the Tribe Areae of the Subfamily Aroideae (Araceae) Based on Sequences of Six Chloroplast Regions

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Abstract*—Typhonium* was recognized as a monophyletic genus in the tribe Areae of the subfamily Aroideae (Araceae) until a recent molecular phylogenetic study indicated that the genus was paraphyletic respective to other Areae genera. However, that phylogenetic study did not discuss the details of infrageneric relationships due to the limited numbers of *Typhonium* samples. To elucidate the phylogenetic relationships in *Typhonium* sensu lato, we conducted phylogenetic analyses based on the combined DNA sequences of six chloroplast regions (3′*trnL–trnF*, *rpl20–*5′*rps12*, *psbB–psbH*, *trnG* intron, *rpoC2–rps2*, and *trnK* 3′intron) from 18 representative *Typhonium* species and additional samples from related genera. The resultant tree strongly suggests that *Typhonium* is not a monophyletic group and that it comprises at least two separate lineages, with other Areae genera nested within, and that *Typhonium* sensu lato may be subdivided into several monophyletic groups. These groups are distinguishable based on the stem-type of shoot organization as well as other morphological characters, which mostly correspond to traditionally recognized taxa. Based on molecular phylogeny and morphology, we proposed a revision of the Areae, wherein *Typhonium* sensu lato is divided into four genera: *Typhonium* sensu stricto, *Sauromatum*, and three new genera, ***Diversiarum***, ***Hirsutiarum***, and ***Pedatyphonium***, which are described here which results in the following combinations: ***Diversiarum diversifolium***, ***Diversiarum alpinum***, ***Pedatyphonium horsfieldii, Pedatyphonium larsenii***, ***Pedatyphonium kunmingense***, ***Pedatyphonium calcicolum***, ***Pedatyphonium omeiense***, ***Hirsutiarum hirsutum***, ***Hirsutiarum brevipilosum***, and ***Sauromatum giganteum***.

***Keywords*—**Areae, *Diversiarum*, *Hirsutiarum*, *Pedatyphonium*, *Sauromatum*, *Typhonium*.

Plants in the genus *Typhonium* Schott (Araceae) are usually small, tuberous or rarely rhizomatous geophytes that demonstrate a diverse morphology. The genus is widely distributed in tropical and subtropical Asia, Africa, the south Pacific region, and Australia (Sriboonma et al. 1994; Mayo et al. 1997, Govaerts and Frodin 2002). Since the monograph of *Typhonium* by Engler (1920), many species have been described, and more than 60 species are now recognized (Govaerts and Frodin 2002; W. L. A Hetterscheid: http://www.aroid.org). The genus has the highest diversity within the tribe Areae R. Br. of the subfamily Aroideae. During the last decade, many new *Typhonium* species have been described from Thailand (Hetterscheid and Boyce 2000; Hetterscheid et al. 2001; Murata et al. 2002; Hetterscheid and Galloway 2006), Vietnam (Hetterscheid and Nguyen 2001; Nguyen 2008), and Australia (Hay 1993, 1997). The area from southeast Asia to Australia is likely to be a center of diversity for the genus (Govaerts and Frodin 2002).

Since Engler (1920), the genus has been classified into tribe Areae together with genera having Euro-Mediterranean distribution (*Arum* L., *Biarum* Schott, *Dracunculus* Mill, *Eminium* Schott, and *Helicodiceros* Schott ex K. Koch), and *Theriophonum* Blume from India and Sri Lanka (Keating 2004). *Heterostalis* (Schott) Schott, which is similar to *Typhonium* but distinct in the shape of the sterile flowers, was reduced to one section of *Typhonium* in Engler's (1920) system. *Sauromatum* Schott, including a few species, has been separated from *Typhonium* for a long time. Murata and Mayo (1990) suspected a generic distinction between them, but recently, Hetterscheid and Boyce (2000) merged *Sauromatum* with *Typhonium*. *Lazarum* was originally described as a monotypic genus (*L. mirable* A. Hay, 1992) endemic to northern Australia but later (Hay 1997) reduced to a synonym of *Typhonium*. Thus, in recent classifications, *Typhonium* has been recognized as a group of rather broad circumscription including several previously recognized groups. Hay (1993) suggested that the genus may be paraphyletic, due to high morphological diversity overlapping with other genera.

For *Typhonium* and its related genera in the tribe Areae, Murata (1990) observed and compared the shoot morphology including the number of leaves per shoot, the position of foliage leaves and cataphylls, the position of the lateral continuation shoot, nature of axillary buds and phyllotaxis, and the pattern of shoot extension. Based on differences in shoot morphology, he recognized four types of stems (types A–D; Table 1) and proposed several groups in the genus that are inconsistent with Engler's (1920) sections. Although Murata (1990) reported only three stem-types (B–D) from *Typhonium*, type A was later observed in *Typhonium* (Sriboonma et al. 1994). Hay (1993) recognized four different groups within the Australian species based on morphological features. Sriboonma et al. (1994) examined several morphological characters including pollen morphology and chromosome number, and analyzed the relationships of *Typhonium* species based on the morphological data. As a result, they revised the classification of *Typhonium* and recognized five sections in the genus: section *Typhonium*, section *Gigantea* Sriboonma et J. Murata, section *Hirsuta* Sriboonma et J. Murata, section *Diversifolia* Sriboonma et J. Murata, and section *Pedata* Sriboonma et J. Murata.

A molecular assessment of the phylogenetic relationships of *Typhonium* was first conducted using chloroplast DNA restriction fragment length polymorphism (RFLP; Sriboonma et al. 1993). The result supported the groups proposed by Murata (1990) based on a comparative study of shoot organization. However, the resultant RFLP tree did not demonstrate the monophyly of *Typhonium*, and the phylogenetic relationships between *Typhonium* and its related genera were unclear due to the paucity of samples and phylogenetic information. A more recent molecular phylogeny based on chloroplast nucleotide sequences (*trnL–trnF* and *rpl20–*5′*rps12* regions) and mitochondrial DNA (*nad1* b/c intron) indicated that *Typhonium* is paraphyletic and that several closely related smaller genera in

Table 1. Summarized characteristics of the stem-type recognized by Murata (1990).

Stem-type	A	B	C	D
Number of leaves per sympodial unit of shoot	At least four	At least four	Two	Three
Mode of shoot extension	Dormancy; whole one or rarely two sympodial units extends at once	Dormancy; the upper part of a sympodial unit and the lower part of the next one extend simultaneously	No dormancy	No dormancy
Apparent position of lateral continuation shoot	At the penultimate node	At the penultimate node	At the penultimate node	Above the ultimate node
Accessory bud	Present	Present	Absent	Absent

the tribe Areae may be recognized within *Typhonium* (Renner and Zhang 2004). However, the results of Renner and Zhang (2004) were not useful for further systematic consideration of *Typhonium* because of the small number of *Typhonium* samples (five species), although their study covered many genera of the tribe Areae.

To assess the relationships among the five sections of *Typhonium* proposed by Sriboonma et al. (1994) and its allied genera, we conducted a phylogenetic analysis using the nucleotide sequences of six chloroplast regions (3′*trnL–trnF*, *rpl20*–5′*rps12*, *psbB–psbH*, *trnG* intron, *rpoC2–rps2*, and *trnK* 3′ intron) for representative species encompassing the diversity of *Typhonium* and its related genera.

Materials and Methods

***Taxon Sampling*—**In total, 19 accessions from 17 *Typhonium* species representing the five sections (nearly 30% of the genus) of Sriboonma et al. (1994) and *T. venosum* (Dryand ex Aiton) Hett. & P. C. Boyce, a representative species of *Sauromatum* that was included in *Typhonium* by Hetterscheid and Boyce (2000), were sampled from natural populations and cultivated plants in the Botanical Gardens of the University of Tokyo (Appendix 1). Because *T. horsfieldii* (Miq.) Steenis as described by Sriboonma et al. (1994) is a polytypic species with a wide geographical range, this species and three synonymous taxa (*T. calcicolum* C. Y. Wu ex H. Li, Y. Shiao & S. L. Tseng, *T. kunmingense* H. Li, and *T. larsenii* S. Y. Hu) are treated separately here. *Typhonium cordifolium* Hu, which was newly recorded from Myanmar based on Tanaka et al. (2006), is also separated from *T. violifolium* Gagnep. In addition, a new species from Myanmar is currently in preparation by the last author of this report. Unfortunately, we were unable to include species from Australia. Four related genera in the tribe Areae (*Arum*, *Biarum* and *Helicodiceros*, and *Theriophonum*) were also used. Based on the recent results of Renner and Zhang (2004) and Cabrera et al. (2008), representative species from *Arisaema* Mart. and *Pinellia* Ten. in the Arisaemateae Nakai, and *Alocasia* Raf., *Colocasia* Schott and *Remusatia* Schott, in the Colocasieae (Schott) Brongn. were used as outgroup taxa in the phylogenetic analyses (Appendix 1).

***DNA Extraction, Amplification, and Sequencing*—**Silica gel dried leaf tissue was ground into powder, and the powder was washed in HEPES buffer (Setoguchi and Ohba 1995) to remove polysaccharides and polyphenols. The washed powder was incubated at 60°C for 30 min with 550 µl extraction solution of 500 µl CTAB buffer (Doyle and Doyle 1990) and 50 µl lysis buffer (10% N-lauroylsarcosine sodium salt, 0.1 M Tris-HCl buffer (pH 8.0), 0.02 M EDTA), and the solution were then extracted by phenol/chloroform/isoamyl alcohol (25:24:1; Nippon Gene, Tokyo). Total genomic DNA was precipitated first with ice-cold isopronanol and subsequently with ice-cold 70% ethanol. Nucleotide sequences of six chloroplast regions were determined by direct sequencing methods following polymerase chain reaction (PCR). Amplification was carried out using TaKaRa ExTaq (TaKaRa Bio, Shiga, Japan), and cycling conditions were 96°C for 45 sec, then 30 cycles of 96°C for 45 sec - 52°C for 45 sec - 72°C for 1 min, and finally 72°C for 10 min. The following primers were used for PCR amplification: trnL-e (5′–GGTTCAAGTCCCTCTATCCC–3′) and trnF-f (5′–ATTTGAACTGGTGACACGAG–3′) of Taberlet et al. (1991) for 3′*trnL–trnF*, rpl20 (5′–TTTGTTCTACGTCTCCGAGC–3′) and 5′-rps12 (5′–GTCCAGGAACATGTACTAGG–3′) of Hamilton (1999) for *rpl20*–5′*rps12*, forward (5′–GATTAGCAATCCGCCGCTTT–3′) and reverse (5′–TTACCACTAAACTATACCCGC–3′) of Xu et al. (2000) for *psbB–psbH*, forward (5′–GCGGGTATAGTTTAGTGGTA–3′) and reverse (5′–CCTCTGTCCTATCCATTAGAC–3′) of Kitano et al. (2005) for *trnG* intron, forward (5′–GTCATATATTTGATCCCGCC–3′) and reverse (5′–CGAGTTTTAGCAAAAGCTGC–3′) of Kitano et al. (2005) for *rpoC2–rps2*, and 7B-Aroid (5′–TATTAGGGCATCCTATTA–3′, designed on the *matK* gene in this study) and trnK-2R (5′–AACTAGTCGGATGGAGTAG–3′) of Johnson and Soltis (1994) for *trnK* 3′intron. Amplification products were purified using the GeneClean III DNA purification Kit (BIO 101, Carlsbad, California, USA) or ExoSAP-IT (GE Healthcare UK Ltd., Buckinghamshire, England). Purified PCR fragments were amplified using the ABI PRISM Big Dye Terminator v3.1 (Applied Biosystems, Foster City, California). Sequencing reactions were performed using the same primers as those used for PCR amplification. Because the *rpl20*–5′*rps12* and *rpoC2–rps2* regions included mononucleotide repeats (poly-A or poly-T), the following sequencing primers were newly designed, *rpl20*–300F (5′–GATTCCTTCGTTTCTATGGT–3′) and *rps12*–300R (5′–AGAGAGGACCTCVCCGTTT–3′) for the former, and *rps2*–Ty (5′–TCCTAGTACCATGACC–3′) and *rpoC2*–Ty (5′–CTCGG TAGAAAGTTCC–3′) for the latter. DNA sequencing was performed using an ABI PRISM 377 DNA sequencer (Applied Biosystems). The program AutoAssembler (Applied Biosystems) was used to assemble complementary sequences. Sequences determined in the present analysis were registered with the DNA Data Bank of Japan (DDBJ), which is linked to GenBank (Appendix 1).

***Sequence Alignments*—**For each of the six regions, multiple sequences were aligned manually for phylogenetic analyses. Gap coding was employed for maximum parsimony (MP) analysis. Each gap of a single nucleotide indel, multinucleotide units (cf. "———" vs. "GTTC"), multinucleotide repeat units (cf. "CTAAG———" vs. "CTAAGCTAAG") and inverted repeat units (cf. "TTTTAAT" vs. "ATTAAA") was coded by binary states "0 or 1" as an unweighted fifth character in the matrix for MP analysis. In addition, when a substitution or a gap was found among nucleotide sequences in the position of other gaps, "N" was added to the position of substitution or gap-state in the gap to reflect its change in the analyses. Length polymorphisms caused by mononucleotide repeats (poly-A or poly-T) and portions that could not be aligned due to ambiguities in alignments were excluded from the analyses. The complete data matrix is available from TreeBASE (study number S2527).

***Phylogenetic Analyses*—**Prior to the tree searches, to test conflicts among different regions, incongruence length difference (ILD) was evaluated by using a partition-homogeneity test in PAUP* version 4.0b10 G4 (Swofford 2002) on a Mac PowerBook running MacOS9. First, for each of the six regions, two-way ILD tests between each single region and all others were conducted on both 15 pairs excluding gaps and 15 pairs including the coded gaps, and then six-way ILD tests were also conducted on each of combined matrixes of six regions excluding and including the coded gaps. Each test was run by 1,000 replicates using a heuristic search with 10 replicates of random sequence addition, tree-bisection-reconnection (TBR) branch swapping, MulTrees option, and 100 trees of MaxTrees. In addition, we visually compared the tree topology of each single region obtained with MP and maximum likelihood (ML) methods using PAUP* software. In the MP analysis, both nucleotide substitutions and coded gaps were used with equal weighting. To search for the shortest trees, MP analysis was performed using a heuristic search with 100 replicates of random sequence addition, TBR branch swapping, and MulTrees option. The limit of MaxTrees was set to no upper limit. The strict consensus tree of the most parsimonious trees was generated, and character changes (substitutions and gaps) were reconstructed on the tree with ACCTRAN character optimization using PAUP* software. MP bootstrap analysis was conducted using 1,000 replicates and the same tree search procedure as described above, except with simple addition sequences. In ML analysis,

TABLE 2. Characteristics of nucleotide sequences and phylogenetic statistics for six cpDNA regions from the analysis of *Typhonium* sensu lato and its related genera.

	3′trnL–trnF	*rpl20–5′rps12*	*psbB–psbH*	*trnG* intron	*rpoC2–rps2*	*trnK 3′* intron	Combined
Length (bp)	406–444	774–846	678–700	872–893	885–915	595–611	4,239–4,341
Aligned length (bp)	476	895	713	977	938	644	4,668
Substitution sites/parsimony informative sites (%; sites per aligned length)	56/28 (11.8/5.9)	84/35 (9.4/3.9)	72/30 (10.1/4.2)	111/42 (11.4/4.3)	75/43 (8.0/4.6)	64/31 (9.9/4.8)	462/209 (9.9/4.5)
Coded gap sites/parsimony informative gap sites (%; sites per aligned length)	9/5 (1.9/1.1)	15/7 (1.7/0.8)	7/6 (1.0/0.8)	13/7 (1.3/0.7)	8/5 (0.9/0.5)	5/2 (0.8/0.3)	57/32 (1.2/0.7)
MP analysis (including coded gaps)							
No. of MP tree (tree length)	1 (73)	4 (127)	12,767 (114)	20 (159)	18,132 (106)	5 (79)	24 (671)
Consistency index (Rescaled consistency index)	0.9315 (0.8809)	0.8425 (0.7473)	0.7544 (0.6024)	0.8365 (0.7170)	0.8302 (0.7143)	0.8861 (0.8142)	0.8227 (0.7047)
ML analysis (excluding coded gaps)							
Best-fit model by AIC	TVM	TVM + I + G	K81 uf + I + G	GTR + G	GTR + I + G	TVM + I	TIM + I + G
Best likelihood score (-ln)	1,072.36776	1,968.20863	1,714.16159	2,309.47976	1,946.08025	1,368.39431	10,660.01860

the best model and the parameter values for each matrix were estimated, based on substitutions only, by Akaike's information criterion (AIC) in the program Modeltest 3.7 (Posada and Crandall 1998). Maximum likelihood heuristic searches were conducted using 100 replicates with random sequence addition. ML bootstrap analysis was conducted using 1,000 replicates and the same tree search procedure as described above, except with as-is addition sequences. In both MP and ML, topologies of the six regions were not discordant, although the basal relationships of several trees were not clearly resolved or were polytomic. Therefore, the phylogenetic analyses shown here were based on the combined sequences of the six regions, using the same settings for the individual genes tree search.

RESULTS

The characteristics of the nucleotide sequences of the six regions from all accessions and phylogenetic information from each analysis are summarized in Table 2. The sequence lengths of the six regions were variable (406–444 bp in 3′*trnL–trnF*, 774–846 bp in *rpl20–5′rps12*, 678–700 bp in *psbB–psbH*, 872–893 bp in *trnG* intron, 885–915 bp in *rpoC2–rps2*, and 595–611 bp in *trnK* 3′intron). Each region included 4–6% parsimony-informative substitution sites, and several coded gaps were also parsimony-informative. The MP and ML phylogenetic trees for each individual region were unresolved due to the paucity of phylogenetic information (data not shown). The partition-homogeneity tests by two-way ILD tests showed a wide range of *p* values on both 15 pairs excluding gaps and 15 pairs including the coded gaps and their average were $p = 0.5118$ and $p = 0.5145$, respectively (Table 3). The tests by six-way ILD test showed $p = 0.572$ for the matrix including gaps, and $p = 0.381$ for the matrix excluding the coded gaps (Table 3). These results did not necessarily indicate incongruence between the different regions. In fact, visual comparison among tree topologies for the six regions yielded no significant incongruence among them. Therefore, nucleotide sequences of all these regions were combined to perform phylogenetic analyses. The final length of the combined dataset ranged from 4,239–4,341 bp, and the aligned length was 4,668 bp. The final matrix included 462 variable sites and 209 parsimony-informative substitution sites. In the MP analysis, 57 coded gaps, of which 32 were parsimony-informative, were added

TABLE 3. Results of a partition-homogeneity test by the two-way and six-way ILD test on each of matrixes excluding gaps and including the coded gaps.

	excluding gaps	including the coded gaps
Two-way ILD test		
3′*trnL–trnF* vs. *rpl20–5′rps12*	0.359	0.350
vs. *psbB–psbH*	0.611	0.891
vs. *trnG* intron	0.284	0.191
vs. *rpoC2–rps2*	0.667	0.906
vs. *trnK* 3′ intron	0.632	0.158
*rpl20–5′rps12*vs. *psbB–psbH*	0.138	0.487
vs. *trnG* intron	0.123	0.094
vs. *rpoC2–rps2*	0.121	0.191
vs. *trnK* 3′ intron	0.479	0.177
psbB–psbH vs. *trnG* intron	0.618	0.722
vs. *rpoC2–rps2*	0.857	0.995
vs. *trnK* 3′ intron	0.950	0.956
trnG intron vs. *rpoC2–rps2*	0.539	0.831
vs. *trnK* 3′ intron	0.641	0.276
rpoC2–rps2 vs. *trnK* 3′ intron	0.658	0.492
Average	0.5118	0.5145
Standard deviation	0.3139	0.2410
Six-way ILD test	0.381	0.572

into the matrix. As a result, 24 most parsimonious trees of 671 steps with CI = 0.8227 and RC = 0.7047 were obtained and their strict consensus tree was generated (Fig. 1). The ML phylogenetic tree was constructed using the best-fit model TIM + I + G, and a single optimal tree with –lnL = 10,660.01860 was obtained (data not shown). Tree topology of the MP strict consensus tree was identical to that of ML optimal tree.

Both MP and ML trees strongly supported the monophyly of the tribe Areae in the subfamily Aroideae (bootstrap values [BS] = 99% for both MP and ML), and showed that the genus *Typhonium* is not monophyletic. The tribe Areae consisted of two major lineages with strong support: clade I corresponding to *Typhonium* sect. *Typhonium* according to Sriboonma et al. (1994) (BS = 100% for both MP and ML) and clade II comprising other species of *Typhonium* and the rest of the genera from tribe Areae (BS = 100% for MP and 98% for ML). Clade II includes several lineages, one of them, comprising the genus *Theriophonum* (clade III; BS = 100% for both MP and ML) was sister to all remaining taxa (clade IV; BS = 92% for MP and 87% for ML). In clade IV, a lineage that consisted of two monophyletic sections of Sriboonma et al. (1994), *Diversifolia* (clade V-1; BS = 100% for both MP and ML) and *Pedata* (clade V-2; BS = 100% for both MP and ML), is strongly supported (clade V; BS = 100% for MP and ML). In addition, *Thyphonium giganteum* Engl. of the section *Gigantea* was a sister to *T. venosum* with weak BS (clade VI; BS = 72% for MP and 65% for ML), and the Euro-Mediterranean genera (*Arum*, *Biarum*, and *Helicodiceros*) formed a clade with moderate to weak BS (clade VII; BS = 82% for MP and 66% for ML). However, relationships among lineages within clade IV are still unclear due to an internal polytomy.

Discussion

In this study, increasing the number of *Typhonium* species (up to 18 species) and their chloroplast sequences (over 4,000 bp from six regions) resulted in highly resolved, well-supported phylogenetic relationships for *Typhonium* and other genera in the tribe Areae (Fig. 1). The resultant phylogenetic tree gave new insights into classification of the tribe Areae. The phylogenetic analysis of Renner and Zhang (2004) could not resolve the basal relationship of the tribe Areae, however, our analysis indicates that the Areae are divided into two distinct lineages (clades I and II), corresponding to *Typhonium* section *Typhonium*, and other members of *Typhonium* and its related genera, respectively. This molecular phylogeny clearly indicated that *Typhonium*, as currently circumscribed (*Typhonium* s. l.), is not a monophyletic group comprising at least two separate lineages, with other Areae genera nested within, therefore suggesting the necessity of revising its classification.

The four stem-types of Murata (1990) are recognized as valuable morphological characters to classify in *Typhonium* (Sriboonma et al. 1994). Types A–D were defined by the combination of four characters: number of leaves per sympodial unit of shoot, mode of shoot extension, position of the lateral continuation shoot, and presence/absence of an accessory bud (Table 1). When the stem-types were compared with the obtained phylogenetic relationship, each of them did not necessarily appear as a synapomorphic character (Fig. 1). However, each of the clades detected in the tree could be characterized by a single stem-type. As we discuss below, phylogenetically and morphologically distinct groups corresponding to traditionally recognized sections within the genus were documented.

Clade I corresponding to *Typhonium* section *Typhonium*, characterized by stem-type D (Sriboonma et al. 1994), was robust with a high support value. More than 30 species were recognized in this section (Sriboonma et al. 1994), and most of the species later described by Hetterscheid and Nguyen (2001) and Hetterscheid et al. (2001) are also considered to be the members of this group. The species of the section are widely distributed in Asia extending to Australia and Africa, and they are also diverse in morphology and chromosome number ($2n$ = 16, 18, 20, 36, and 52). In clade I, most subclades were only weakly supported, with the exception of the *T. roxburghii* Baker and "*T.* sp. nov." clade, and the relationships among species were unresolved. As this group seems to be phylogenetically complex, a more detailed phylogenetic study for more species including Australian species will be needed to resolve species relationships within the clade.

Clade II, including a wide range of taxa of the tribe Areae, was also robust with high support values, but it could not be discriminated by synapomorphic morphological characters. It was subdivided into two clades (III and IV), and clade III corresponds to the genus *Theriophonum*. In clade IV, four lineages might be recognized (V, VI, VII, and *Typhonium hirsutum*). Of these, clade V consists of *Typhonium* species commonly characterized by pedate leaves, thick and narrowly conical interstices on the inflorescence axis, and a basic chromosome number of n = 13. Clade V includes two lineages that correspond to *Typhonium* sections *Diversifolia* (clade V-1) and *Pedata* (clade V-2) of Sriboonma et al. (1994), which are associated with stem-types A and C, respectively. In addition, the former section is characterized by having capitate sterile flowers. The latter includes a subclade of *T. horsfieldii* and its allied species (*T. horsfieldii* complex). Although Sriboonma et al. (1994) mentioned that it is difficult to separate these species on the basis of morphology, *T. horsfieldii* and three allied species were distinguishable based on differences in their chloroplast DNA sequences, and a sister relationship between *T. calcicolum* and *T. larsenii* was observed. In addition to the species sampled here, *Typhonium gaoligogense* (Z .L. Wang et H. Li) Hett. & P. C. Boyce, which was first described as a species of *Sauromatum* (Wang and Li 1999), is also considered to belong to the *T. horsfieldii* complex. Further examination is needed to discriminate the taxonomic status of species in the *T. horsfieldii* complex.

The remaining *Typhonium* species in clade IV, *T. giganteum*, *T. venosum*, and *T. hirsutum*, are often recognized as morphologically similar species (Murata and Mayo 1990; Hetterscheid and Boyce 2000). Of these species, *T. giganteum* and *T. venosum* showed sister relationship in the molecular phylogeny (clade VI), but the branch support was weak. In previous taxonomies, *Typhonium giganteum* has been classified in section *Gigantea* together with *T. lillifolium* Hay, having a B stem-type (Sriboonma et al. 1994). *Typhonium venosum* has been previously treated as *Sauromatum* [*S. venosum* (Dryand et. Aiton) Kunth] together with the species *T. brevipes* Hook. f. [*S. brevipes* (Hook. f) N. E. Brown], both also have the B stem-type (Murata 1990). Although we need to examine the phylogenetic positions of *T. lillifolium* and *T. brevipes*, it is likely that the species of section *Gigantea* and *Sauromatum* are circumscribed as a distinct group.

On the other hand, *T. hirsutum* has the A stem-type and pedate leaves, but it is not clear in our study which species it is most closely related to. The species was first described as a species of *Arisaema* based on a fruiting specimen, and then moved to *Typhonium* based on the observation of a

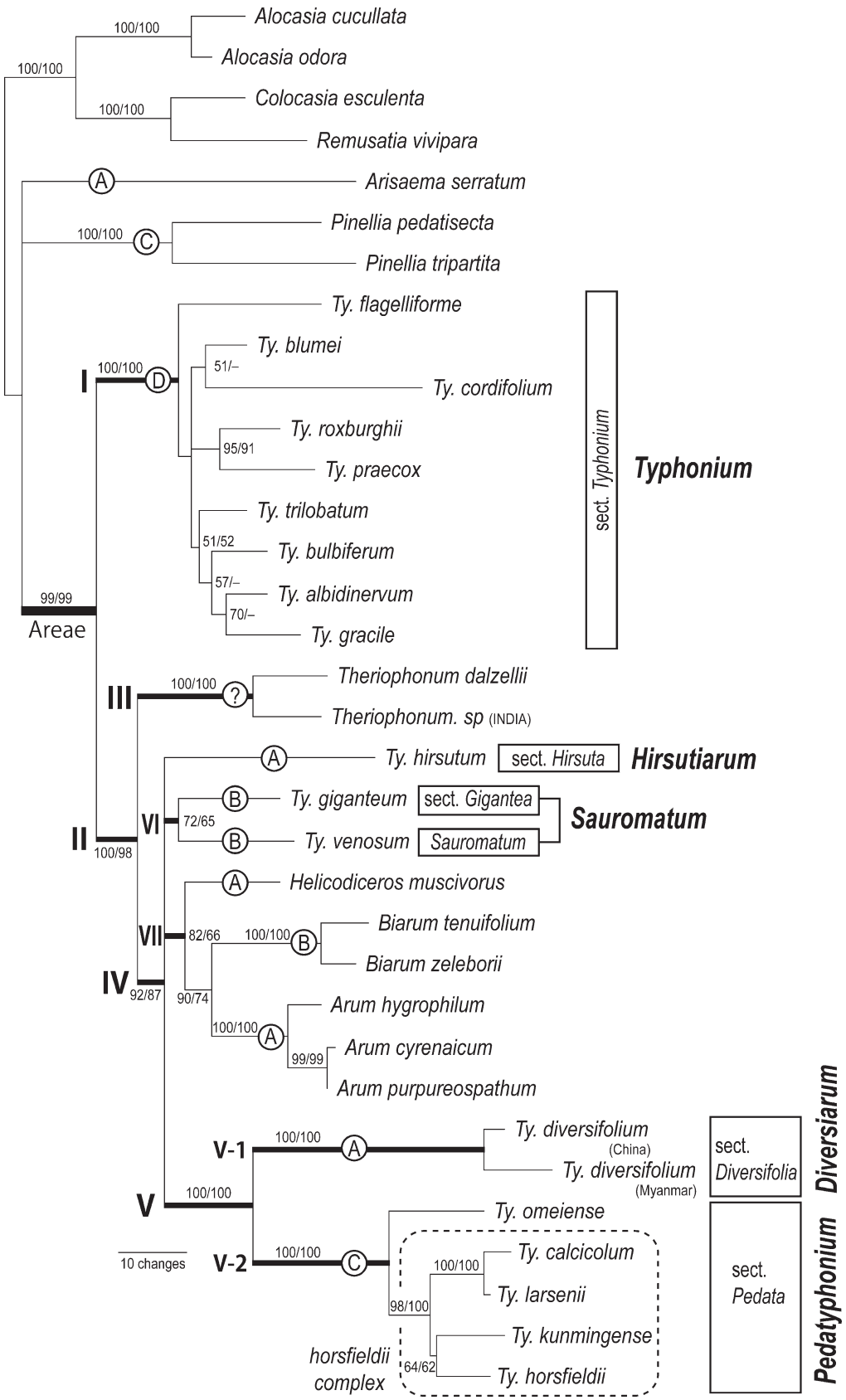

FIG. 1. Strict consensus tree of 24 trees resulting from maximum parsimony (MP) analysis of combined sequences of six chloroplast regions (length = 671, CI = 0.8227, RC = 0.7047). Branch lengths were estimated based on ACCTRAN character optimization using PAUP, and the scale bar is shown. Support values of branches (over 50%) estimated by bootstrap analyses are shown above branches (MP/ML). Branches of major clades with strong support in tribe Areae are drawn as thickened lines, and their names (Areae, clades I, II, III, IV, V, V-1, and V-2) are shown. Circled letters (A, B, C, D) on the branches indicate the stem-type of Murata (1990) (see Table 2), circled question mark (?) indicates "unknown". The sections of *Typhonium* in the sense of Sriboonma et al. (1994) and the genus *Sauromatum* are shown as open box on the right of the tree. The proposed genera in this study are shown in bold italics.

perfect flowering specimen (Murata and Mayo 1990). This species is a member of section *Hirsuta* including the rare species *T. listeri* Prain, which was tentatively included in this section (Sriboonma et al. 1994). The species later described by Hetterscheid and Boyce (2000) as *T. brevipilosum* Hett. et Sizemore is also included in this section.

In clade IV, Euro-Mediterranean elements of the Areae, *Helicodiceros*, *Biarum*, and *Arum*, together formed a monophyletic group (clade VII). Although we could not include the other two genera, *Eminium* and *Dracunculus*, our results along with those of Renner and Zhang (2004) supported the close relationships of the Euro-Mediterranean genera.

The phylogenetic relationships recovered in this study suggest that *Typhonium* s. l. should be subdivided into several monophyletic groups (Fig. 1). Of them, one (clade I) corresponding to the current *Typhonium* section *Typhonium* should be treated as *Typhonium* s. s. For the remaining groups that appeared as clades V-1, V-2, VI, and *Typhonium hirsutum* in clade IV, they could be included in one large genus, together with the Euro-Mediterranean genera (clade VII). Or each of them could be treated as a different genus, because the basal relationship of their clades was unresolved in the detected phylogeny. In considering the stem-type of shoot organization as well as other morphological characters, each of the groups, as is each of the Euro-Mediterranean genera, is clearly circumscribed as a distinct taxon, respectively. In conclusion, based on molecular phylogeny and morphology, we propose a revision of the Areae, wherein *Typhonium* sensu lato is divided into four genera: *Typhonium* (clade I), *Sauromatum* (clade VI), and three new genera: *Diversiarum* (clade V-1), *Pedatyphonium* (clade V-2), and *Hirsutiarum*, which are transferred from *Typhonium* sections *Diversifolia*, *Pedata*, and *Hirsuta*, respectively.

Taxonomic Treatment

Diversiarum J. Murata & Ohi-Toma, stat. nov. et nom. nov. *Typhonium* sect. *Diversifolia* Sriboonma et J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 255–313. 1994.—TYPE: *Typhonium diversifolium* Wall. et Schott, Aroideae 13, t. 20. 1855. [= *Diversiarum diversifolium* (Wall. et Schott) J. Murata & Ohi-Toma]

Two species are distributed in the Himalayas, Myanmar, and China.

1. **Diversiarum diversifolium** (Wall. ex Schott) J. Murata & Ohi-Toma, comb. nov. *Typhonium diversifolium* Wall. ex. Schott, Aroideae: 13, t. 20. 1855.—TYPE: NEPAL. *Wallich's Number. List no. 8933a in 1821* (holotype: K)

2. **Diversiarum alpinum** (C. Y. Wu ex H. Li, Y. Shiao et S. L. Tseng) J. Murata & Ohi-Toma, comb. nov. *Typhonium alpinum* C. Y. Wu ex H. Li, Y. Shiao et S. L. Tseng, Acta Phytotax. Sin. 15: 104. 1977.—TYPE: CHINA, Yunnan, *Diandongbai group 354* (holotype: KUN).

Pedatyphonium J. Murata & Ohi-Toma, stat. nov. et nom. nov. *Typhonium* sect. *Pedata* Sriboonma et J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 255–313. 1994.—TYPE: *Typhonium pedatum* Schott, Bot. Wochenbl. 7: 262. 1857. [= *Pedatyphonium pedatum* (Schott) J. Murata & Ohi-Toma]

At least five species are distributed in China, Myanmar, Thailand, and Indonesia. In the classification of Sriboonma et al. (1994), two species, *Typhonium horsfieldii* and *T. omeiense*, were recognized, and *T. horsfieldii* complex comprised several synonymic taxa. However, this study treated three of the synonymous taxa as one species.

3. **Pedatyphonium horsfieldii** (Miq.) J. Murata & Ohi-Toma, comb. nov. *Sauromatum horsfieldii* Miq., Fl. Ned. Ind. 3: 196. 1855. *Typhonium horsfieldii* (Miq.) v. Steenis, Bull. Bot. Gard. Buitenz., ser. 3, 17: 403. 1948.—TYPE: INDONESIA. Java, *Horsfield s. n.* (holotype: K; isotype: BM).

4. **Pedatyphonium larsenii** (S. Y. Hu) J. Murata & Ohi-Toma, comb. nov. *Typhonium larsenii* S. Y. Hu, Dansk Bot. Arkiv 23: 448. 1968.—TYPE: THAILAND. Chiengmai, *Sorensen, Larsen & Hansen 3931* (holotype: C; isotype: A)

5. **Pedatyphonium kunmingense** (H. Li) J. Murata & Ohi-Toma, comb. nov. *Typhonium kunmingense* H. Li, Acta Phytotax. Sin. 15: 104. 1977.—TYPE: CHINA. Yunnan, *B. Y. Qin 58944* (holotype: KUN).

6. **Pedatyphonium calcicolum** (C. Y. Wu ex H. Li, Y. Shiao et S. L. Tseng) J. Murata & Ohi-Toma, comb. nov. *Typhonium calcicolum* C. Y. Wu ex H. Li, Y. Shiao et S. L. Tseng, Acta Phytotax. Sin. 15: 104. 1977.—TYPE: CHINA. Yunnan, *S. Z. Wang 731* (holotype: KUN).

7. **Pedatyphonium omeiense** (H. Li) J. Murata & Ohi-Toma, comb. nov. *Typhonium omeiense* H. Li, Acta Phytotax. Sin. 15: 105. 1977.—TYPE: CHINA. Sichuan, *J. L. Chuan 2138* (holotype: KUN).

Hirsutiarum J. Murata & Ohi-Toma, stat. nov. et nom. nov. *Typhonium* sect. *Hirsuta* Sriboonma et J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 255–313. 1994.—TYPE: *Arisaema hirsutum* S. Y. Hu, Dansk Bot. Arkiv 23: 454, t. 11. Figures 1–5. 1968. [= *Hirsutiarum hirsutum* (S. Y. Hu) J. Murata & Ohi-Toma].

Two species are distributed in Sumatra of Indonesia, Thailand, and Yunnan province of China. *Typhonium listeri* in Myanmar and India, which was placed in *Typhonium* section *Hirsuta* by Sriboonma et al. (1994), is an unclear species because of a paucity of information.

8. **Hirsutiarum hirsutum** (S. Y. Hu) J. Murata & Ohi-Toma, comb. nov. *Arisaema hirsutum* S. Y. Hu, Dansk Bot. Arkiv 23: 454. 1968. *Typhonium hirsutum* (S. Y. Hu) J. Murata & Mayo, Kew Bull. 46: 129. 1990.—TYPE: THAILAND. *Payap 3939* (holotype: C).

9. **Hirsutiarum brevipilosum** (Hett. & Sizemore) J. Murata & Ohi-Toma, comb. nov. *Typhonium brevipilosum* Hett. & Sizemore, Aroideana 23: 48–55. 2000.—TYPE: INDONESIA. Sumatra, *Hetterscheid H.AR.097-T* (holotype: C).

Sauromatum Schott, Melet. Bot. 17. 1832.—TYPE: *Sauromatum guttaum* (Wall.) Schott. [= *Sauromatum venosum* (Dryand. ex Aiton) Kunth.]

This study treated two taxa, but *T. lillifolium* and *T. brevipes* still need to be examined.

10. Sauromatum venosum (Dryand. ex Aiton) Kunth. Enum. Pl. 3: 28. 1841. *Arum venosum* Dryand. ex Aiton, Hort. Kew 3:315. 1789. *Typhonium venosum* (Dryand. ex Aiton) Hett. & P. C. Boyce, Aroideana 23: 48–55. 2000.—TYPE: *W. Malcolm. s. n.* (holotype: BM)

11. **Sauromatum giganteum** (Engl.) J. Murata & Ohi-Toma, comb. nov. *Typhonium giganteum* Engl., Bot. Jahrb. 4: 66, t. 1. 1883.—TYPE: CHINA. Beijing. *Skatschkow s. n.* (LE).

Key to the Genera of Areae

1. Placenta parietal to subbasal ..... 2.
   2. Leaf blade sagittate or hastate. Ovules more than three. Fruits red ..... *Arum*
   2. Leaf blade imperfectly pedatisect. Ovules 2. Fruits white to pale lilac ..... *Eminium*
1. Placenta basal and/or apical ..... 3.
   3. Placenta basal and apical ..... 4.
      4. Pseudostem distinct. Male zone of spadix contiguous with female zone ..... *Dracunculus*
      4. Pseudostem indistinct. Male zone of spadix separated from female zone by subulate to filiform sterile organs ..... 5.
         5 Spadix appendage with many hair-like filform projections ..... *Helicodiceros*
         5. Spadix appendage smooth ..... *Theriophonum*
   3. Placenta basal ..... 6.
      6. Peduncle directly surrounded by sheath-like leaves. Accessory buds absent on underground stem ..... 7.
         7. Normal leaf pedate or simple, usually 1 per shoot (per season) ..... *Sauromatum*
         7. Normal leaves simple, more than 2 per shoot ..... *Biarum*
      6. Peduncle usually surrounded by normal leaves. Accessory buds present or absent ..... 8.
         8. Sympodial unit triphyllous. Lateral continuation of shoot (next to sympodium) arising above (and opposite to) ultimate leaf (= stem type D) ..... *Typhonium*
         8. Sympodial unit diphyllous or with more than four leaves. Lateral continuation of shoot arising at axil of penultimate leaf ..... 9.
            9. Diphyllous sympodial units extending successively in single season. Accessory bud formed at axil of penultimate leaf (= stem type C) ..... *Pedatyphonium*
            9. Single sympodial unit with more than four leaves extending in single season. Accessory bud not formed (= stem type A) ..... 10.
               10. Leaves glabrous. Distributed in temperate to subalpine regions in the Himalayas and southwestern China ..... *Diversiarum*
               10. Leaves hirsute. Distributed in tropical southeastern Asia ..... *Hirsutiarum*

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Appendix 1. List of accessions used in this study. The accessions of *Typhonium* sensu lato were categorized by proposed genera with sections of Sriboonma et al. (1994). Format: species, geographical origin or source, collector & voucher No., DDBJ accession number for 3′*trnL-trnF*, *rpl20-*

rps12, *psbB-psbH*, *trnG* intron, *rpoC2-rps2*, *trnK* 3′ intron. Voucher specimens are kept in herbarium TI, and some plants are cultivated in Botanical Gardens of the University of Tokyo (BGUT) and Botanical Garden of Setsunan University (BGSU).

Typhonium* s. l.—*Typhonium* (= section *Typhonium*):** *T. albidinervum* C. Z.Tang & H. Li, China, *J. Murata Ty01*, AB494482, AB494516, AB494550, AB494584, AB494618, AB494652. *T. blumei* Nicolson & Sivad., Japan: Okinawa, *J. Murata Ty02*, AB494484, AB494518, AB494552, AB494586, AB494620, AB494654. *T. bulbiferum* Dalzell, India, *S. R.Yadav s. n.*, AB494483, AB494517, AB494551, AB494585, AB494619, AB494653. *T. cordifolium* S. Y. Hu, Myanmar: Mt. Popa, *Ohi-Toma 05071403*, AB494485, AB494519, AB494553, AB494587, AB494621, AB494655. *T. flagelliforme* (Lodd.) Blume, Indonesia, *J. Murata Ty03*, AB494486, AB494520, AB494554, AB494588, AB494622, AB494656. *T. gracile* (Roxb.) Schott, Myanmar, *J. Murata Ty04*, AB494487, AB494521, AB494555, AB494589, AB494623, AB494657. *T.* sp. nov., Myanmar: Kyaiktiyo, *J. Murata Ty06*, AB494490, AB494524, AB494558, AB494592, AB494626, AB494660. *T. roxburghii* Schott, China: Yunnan, *J. Murata 19940812*, AB494488, AB494522, AB494556, AB494590, AB494624, AB494658. *T. trilobatum* (L.) Schott, Philippines, *J. Murata Ty05*, AB494489, AB494523, AB494557, AB494591, AB494625, AB494659. ***Diversiarum* (= section *Diversifolia*):** *T. diversifolium* Wall. ex Schott, China: Yunnan, *J. Murata et al. 021089*, AB494491, AB494525, AB494559, AB494593, AB494627, AB494661; Myanmar, *J. Murata Ty07*, AB494492, AB494526, AB494560, AB494594, AB494628, AB494662. ***Pedatyphonium* (= section *Pedata*):** *T. calcicolum* C. Y. Wu ex H. Li, Y. Shiao & S. L. Tseng, China: Yunnan, *J. Murata 199402*, AB494493, AB494527, AB494561, AB494595, AB494629, AB494663. *T. horsfieldii* (Miq.) Steenis, Indonesia: Bali, *M. Takashima s. n*, AB494494, AB494528, AB494562, AB494596, AB494630, AB494664. *T. kunmingense* H. Li, China: Yunnan, *J. Murata Ty08*, AB494495, AB494529, AB494563, AB494597, AB494631, AB494665. *T. larsenii* S. Y. Hu, Thailand, *T. Yahara s. n.*, AB494496, AB494530, AB494564, AB494598, AB494632, AB494666. *T. omeiense* H. Li, China, *J. Murata Ty09*, AB494497, AB494531, AB494565, AB494599, AB494633, AB494667. ***Hirsutiarum* (= section *Hirsuta*):** *T. hirsutum* (S. Y. Hu) J. Murata & Mayo, Thailand, *J. Murata Ty10*, AB494498, AB494532, AB494566, AB494600, AB494634, AB494668. ***Sauromatum* (= section *Gigantea*):** *T. giganteum* Engl., BGUT from Thailand, *T. Yamazaki s. n.*, AB494499, AB494533, AB494567, AB494601, AB494635, AB494669. *T. venosum* (Dryand. ex Aiton) Hett. & P. C. Boyce, BGUT from Thailand, *J. Murata Ty11*, AB494500, AB494534, AB494568, AB494602, AB494636, AB494670. **Areae—Arum cyrenaicum* Hruby, BGUT, *Ohi-Toma Arum01*, AB494503, AB494537, AB494571, AB494605, AB494639, AB494673. *Arum hygrophilum* Boiss., BGUT, *Ohi-Toma Arum02*, AB494504, AB494538, AB494572, AB494606, AB494640, AB494674. *Arum purpureospathum* P. C. Boyce, BGUT, *Ohi-Toma Arum03*, AB494505, AB494539, AB494573, AB494607, AB494641, AB494675. *Biarum tenuifolium* (L.) Schott., BGSU, *H. Murata Biarum01*, AB494506, AB494540, AB494574, AB494608, AB494642, AB494676. *Biarum zeleborii* Schott, BGSU, *H.Murata Biarum02*, AB494507, AB494541, AB494575, AB494609, AB494643, AB494677. *Helicodiceros muscivorus* Engl., BGUT, *Ohi-Toma Hel01*, AB494508, AB494542, AB494576, AB494610, AB494644, AB494678. *Theriophonum dalzellii* Schott, India: Maharashtra, *S. R.Yadav s. n.*, AB494501, AB494535, AB494569, AB494603, AB494637, AB494671. *Theriophonum* sp., India: Kerala, *S. R.Yadav s. n.*, AB494502, AB494536, AB494570, AB494604, AB494638, AB494672. ***Outgroup*—Arisaemateae:** *Arisaema serratum* (Thunb.) Schott, Japan: Chiba, *Ohi-Toma Arisa222*, AB494509, AB494543, AB494577, AB494611, AB494645, AB494679. *Pinellia pedatisecta* Schott, BGUT, *Ohi-Toma Pin01*, AB494510, AB494544, AB494578, AB494612, AB494646, AB494680. *Pinellia tripartita* Schott., BGUT, *Ohi-Toma Pin02*, AB494511, AB494545, AB494579, AB494613, AB494647, AB494681. **Colocasieae:** *Alocasia cucullata* Schott, BGUT, *Ohi-Toma Alo01*, AB494512, AB494546, AB494580, AB494614, AB494648, AB494682. *Alocasia odora* Schott, BGUT, *Ohi-Toma Alo02*, AB494513, AB494547, AB494581, AB494615, AB494649, AB494683. *Colocasia esculenta* (L.) Schott, BGUT, *Ohi-Toma Col01*, AB494514, AB494548, AB494582, AB494616, AB494650, AB494684. *Remusatia vivipara* Schott, Myanmar, *Tanaka et al. 23522*, AB494515, AB494549, AB494583, AB494617, AB494651, AB494685.