A phylogeny of the Areae (Araceae) implies that *Typhonium*, *Sauromatum*, and the Australian species of *Typhonium* are distinct clades

Natalie Cusimano,[1] Matthew D. Barrett,[2,3] Wilbert L.A. Hetterscheid[4] & Susanne S. Renner[1]

1 *Department of Biology, University of Munich, 80638 Munich, Germany*
2 *Botanic Gardens and Parks Authority, Fraser Ave, West Perth, Western Australia 6005*
3 *School of Plant Biology, University of Western Australia, Crawley, Western Australia 6009*
4 *Von Gimborn Arboretum, Velperengh 13, 3941 BZ Doorn, The Netherlands*
Author for correspondence: *Natalie Cusimano, cusimano@bio.lmu.de*

Abstract With in excess of 70 species, the Southeast Asian/Australian genus *Typhonium* is the largest genus of the Areae, a tribe that includes up to nine smaller genera of which *Sauromatum* and *Lazarum* have recently been reduced to the synonymy of *Typhonium*. To test the circumscription and relationships of *Typhonium* to the other Areae, we used chloroplast and nuclear DNA sequences (4319 aligned nucleotides) for 86 of the total 153 species, including representatives of all relevant genera. In the resulting phylogeny, *Typhonium* species fall into three well-supported clades: the first comprises most *Typhonium* species, including the type, *T. trilobatum*; the second consists of the type of *Sauromatum*, *S. guttatum*, and other species formerly placed in that genus; the third includes only Australian endemics. Each of the remaining six genera of Areae is monophyletic. *Sauromatum* and *Typhonium* are not sister groups, requiring the recognition of *Sauromatum*. The Australian clade also needs to be ranked as a genus to achieve similar levels of morphological, geographic, and genetic distinctness among the genera of Areae. However, since only 10 of the 16 described Australian endemics currently placed in *Typhonium* have so far been sequenced, not including the type of the name of the Australian genus *Lazarum*, we refrain from applying this name to the Australian clade. Among the nomenclatural and taxonomic results of this study are a key to the nine species of *Sauromatum*, and five new combinations. We also report two new chromosome counts and discuss the implications of the molecular phylogeny for the evolution of *Sauromatum* karyotypes.

Keywords Areae; chromosome numbers; *Lazarum*; molecular phylogenetics

■ INTRODUCTION

The tribe Areae (Araceae) in its current circumscription comprises seven genera (Hay, 1997; Mayo & al., 1997; Hetterscheid & Boyce, 2000) and at least 153 species (including 14 awaiting description). The Areae range from Australia to Europe, with one species in Africa, and a center of diversity in SE Asia, another in the Mediterranean region and the Near East. Two genera, the SE Asian *Sauromatum* and the Australian *Lazarum*, have recently been sunk into *Typhonium*, the largest genus of the tribe. The monophyly of this broadly circumscribed *Typhonium*, however, appears doubtful. An early DNA restriction fragment analysis that included eight species of *Typhonium* (five of these now belonging to *Sauromatum*) and representatives of two other Areae genera found *Typhonium* paraphyletic (Sriboonma & al., 1993). A concurrent morphological cladistic analysis of 36 species of *Typhonium* (including six here shown to belong in *Sauromatum*) and one *Arum* species yielded the same result (Sriboonma & al., 1994). That *Typhonium* and *Sauromatum* might be distinct clades was suggested by the family-wide restriction fragment analysis of French & al. (1995) in which the single species of *Typhonium* and *Sauromatum* included did not form a clade, but instead a grade with *Theriophonum* falling in between (*Lazarum* was not included). A more recent chloroplast phylogeny for Areae that included five species of *Typhonium* (three of these here shown to belong in *Sauromatum*), and numerous other Areae, yielded the same result (Renner & Zhang, 2004). None of these molecular studies, however, sampled a sufficient number of species to properly test the monophyly of *Typhonium*.

The genus *Sauromatum* was erected by Heinrich Wilhelm Schott (1832: 17) to accommodate *S. guttatum* (Ait.) Schott (*Arum guttatum* Ait.) and *S. pedatum* (Link & Otto) Schott (*Arum pedatum* Link & Otto), two obviously related entities from the understory of monsoon forests in India. Kunth (1841) transferred *Arum venosum* Dryand ex Ait., a species described from a cultivated specimen, to *Sauromatum* (this species is now considered conspecific with *S. guttatum* and *S. pedatum*). Shortly thereafter, Miquel (1855, 1864) added *S. pulchrum* from Sumatra and *S. horsfieldii* from Central Java. The last was transferred to *Typhonium* by van Steenis (1948) who considered it to be the same as *T. fallax* N.E. Br. and *T. pedatum* Engl. Another species moved between *Sauromatum* and *Typhonium* is *T. brevipes* (Hooker, 1893) from Sikkim in the southern Himalayas (Brown, 1903). Of these doubtfully assigned species, two are widely cultivated, *S. venosum*, the commercial curiosity marketed as the 'voodoo lily,' and *S. giganteum*, in spite of the vile scent they produce at peak flowering.

The most important characters used by Schott (1832) to distinguish his *Sauromatum* from *Typhonium* were the connate

spathe tube, ovaries with two (rather than one) ovules, scattered staminodes and a short peduncle in *Sauromatum*. In addition, Schott noted that *Sauromatum* produced leaves after flowering, whereas *Typhonium* produced them before or during flowering. The later discovery of intermediate forms, however, diluted these generic differences. Thus, partly fused spathe tubes are found in *S. hirsutum* (see below) and a fused spathe tube, but with leaves appearing during flowering, in *S. brevipes*, resulting in the above described transfers (e.g., Brown, 1903; van Steenis, 1948; Hetterscheid & Boyce, 2000). The problem of generic assignments was exacerbated by incompletely known species. For example, a fruiting specimen of *T. hirsutum* was discovered in 1958 in dry evergreen forest in Chiang Mai (Thailand) at an altitude of 1130 m and described as *Arisaema hirsutum* by Hu (1968). Some 30 years later, Murata & Mayo (1991) realized that a flowering specimen represented the same species; however, they thought it better placed in *Typhonium*, with "some interesting resemblances to its neighboring genus *Sauromatum*," such as the spathe tube fused for up to one quarter of its length and an inflorescence intermediate between *T. giganteum* and *S. venosum*. A fuller understanding of many species of *Typhonium* and *Sauromatum* was only achieved once they were brought into cultivation (Hetterscheid & al., 2001). Nevertheless, the apparently impossible morphological separation of *Sauromatum* and *Typhonium* caused Hetterscheid & Boyce (2000) to sink *Sauromatum* into *Typhonium*.

The other genus whose relationship to *Typhonium* has been difficult to assess from morphology alone is *Lazarum*. This is a monotypic entity based on an Australian species discovered on Melville Island near Darwin (Northern Territory) in 1984 (Hay, 1992). *Lazarum mirabile* resembles *Sauromatum*, *Typhonium*, and *Biarum*. It differs from these genera in its connate spathe tube with two chambers divided by an annular septum. After the discovery of another species from Darwin, *T. praetermissum*, with spathe tube characters intermediate between *Lazarum mirabile* and "typical" *Typhonium*, *L. mirabile* was transferred to *Typhonium* (Hay, 1997).

Here we test the monophyly and relationships of *Typhonium* based on a dense species sampling consisting of 86 species of Areae selected to represent all geographically and morphologically distinct groups of *Typhonium* and its relatives; we specifically included most of the species ever placed in *Sauromatum*. It turns out that *Typhonium* in its broad circumscription is a polyphyletic group composed of three distinct clades. We present the phylogenetic results and formalize some of the nomenclatural changes required by our findings. We also report new chromosome numbers and discuss the implications of the molecular phylogeny for the evolution of *Sauromatum* karyotypes. Finally, we present a key to the species of our redefined *Sauromatum*.

■ MATERIALS AND METHODS

Taxon sampling and sequencing. — We sampled 86 of the 153 species of Areae. The Areae comprise *Arum* with 29 species (Boyce, 1993, 2006; Lobin & al., 2007), *Biarum* with 21 (Boyce, 2008), *Dracunculus* with 2 (Mayo & al., 1997), *Eminium* with 9 (Mayo & al., 1997; Bogner & Boyce, 2008), *Helicodiceros* with 1 (Mayo & al., 1997), *Theriophonum* with 5 (Sivadasan & Nicolson, 1982; Mayo & al., 1997), *Typhonium* s.l. with 72 species (Hay, 1993, 1997; Sriboonma & al., 1994; Hay & Taylor, 1996; Sookchaloem & Murata, 1997; Hetterscheid & Boyce, 2000; Hetterscheid & Nguyen, 2001; Hetterscheid & al. 2001; Murata & al., 2002; Wang & al., 2002; Hetterscheid & Galloway, 2006; Dao & al., 2007; Nguyen, 2008: this number includes species here shown to belong in *Sauromatum* or the Australian clade), and at least 14 as yet undescribed species belonging to various of these genera. For this study, we included 52 species of *Typhonium* s.l., 18 of *Arum*, 9 of *Biarum*, 2 each of *Eminium* and *Theriophonum*, both *Dracunculus* species, and the single species of *Helicodiceros*. Several species of *Typhonium* are represented by two or three accessions. As outgroups, we used two species of *Arisaema* based on the chloroplast phylogeny of Renner & Zhang (2004). This totals to 88 species, represented by 98 accessions. All species with their sources and herbarium vouchers (where applicable) are listed in the Appendix.

To deduce phylogenetic relationships, we relied on a nuclear locus, the phytochrome C gene (*PhyC*), and two chloroplast loci, the *rpl20-rps12* intergenic spacer and the tRNA*Lys* gene (*trnK*), which contains a group I intron that encodes the maturase K (*matK*) open reading frame. Total DNA from silica-dried leaves was extracted with the NucleoSpin plant kit according to the manufacturer's protocol (Macherey-Nagel, Düren, Germany). Sequencing of the ca. 2300 nucleotide (nt)-long *trnK* marker, amplified in one piece with the primer pair trnK-3914F (dicot)–trnK-16R (Johnson & Soltis, 1994), was problematic. Consequently, we designed new internal primers and amplified the section in two pieces: trnK-3914F–trnK-RM and trnK-FM– trnK-16R. The new primer sequences are as follows: trnK-RM 5′-AAGATGTTGATCGTAAATAAGAGG-3′ and trnK-FM 5′-GTTTTGCTGTCATTATGGAAATTCC-3′. *PhyC* was also amplified in two pieces with the newly designed primers: A20F–750R and 430F–AR: A20F: 5′-CACTCAATCCTACAAACTGGC-3′, 750R: 5′-AGATCCATAACATTTGGTGATTGT-3′, 430F: 5′-CTCGTGATGTCTGTCACAATAAG-3′ and AR: 5′-GAATAGCATCCATTTCAACATC-3′. The *rpl20-rps12* intergenic spacer was amplified using the primers and PCR conditions described in Renner & Zhang (2004).

Polymerase chain reactions (PCR) were performed with 10 µM primers in 25 µl reactions, using BioTherm DNA polymerase (Genecraft, Lüdinghausen, Germany). The initial step of 5 min at 95°C was followed by 35 cycles of 95°C for 30 s for DNA denaturation, 60°C for 60 s for primer annealing, and 72°C for 2 min and 40 s for primer extension. PCR products were controlled by electrophoresis on an ethidium bromide-stained 1% agarose gel with the Lambda DNA size marker. PCR products were purified using either Promega Wizard® SV Gel and PCR Clean-Up System or Agencourt AMPure® PCR purification kit and quantified electrophoretically, using Lambda DNA as standard. If multiple bands were detected, an additional electrophoresis was performed to excise and analyze them separately. Sequencing relied on Big Dye Terminator kits

(Applied Biosystems, Warrington, U.K.) and the amplification primers. Cycle sequencing products were cleaned by Sephadex G-50 Superfine gel filtration (Amersham, Uppsala Sweden) on MultiScreen TM-HV membrane plates (Millipore, Bedford, U.S.A.) according to the manufacturers' protocols to remove unincorporated nucleotides. Fragments were separated on an ABI 3100 Avant capillary sequencer, assembled and edited using the software Sequencher (Gene Codes, Ann Arbor, Michigan, U.S.A.), and BLAST-searched in GenBank. Sequences are deposited in GenBank (for accession numbers see Appendix).

Alignments and phylogenetic analyses. — Alignments (Table 1) were generated in MacClade (Maddison & Maddison, 1992) and continuously adjusted manually. The three data partitions were first analyzed separately, and in the absence of statistically supported topological contradictions (>80%), they were then combined.

Phylogenetic inference of the combined data (4319 aligned nucleotides) relied on maximum likelihood (ML) as implemented in the RAxML BlackBox (Stamatakis & al., 2008, http://phylobench.vital-it.ch/raxml-bb/) and on Bayesian analysis as implemented in MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Bootstrapping under ML used 1000 replicates performed in RAxML. All searches relied on the GTR + G model, with model parameters estimated during runs. (RAxML uses the GTRCAT approximation of the GTR + G model, with the gamma shape parameter having 25 rate categories.)

Bayesian runs were started from independent random starting trees and repeated four times. Markov chain Monte Carlo runs extended for 2 million generations, with trees sampled every 2000th generation (resulting in 1001 trees for each run). We used a flat Dirichlet prior for the relative nucleotide frequencies and rate parameters, a discrete uniform prior for topologies, and an exponential distribution (mean 10) for the γ-shape parameter and all branch lengths. Convergence was assessed by checking that (1) final likelihoods and majority rule topologies among runs were similar; (2) the standard deviations (SD) of split frequencies were <0.01; (3) the convergence diagnostic (the potential scale reduction factor given by MrBayes) approached 1; and (4) by examining the plot provided by MrBayes of the generation number versus the log probability of the data. TRACER (Rambaut & Drummond, 2007) was used to assess whether runs had reached convergence. Trees saved prior to convergence were discarded as burn-in (100 trees) and a consensus tree constructed from the remaining 3604 trees.

Chromosome counts. — Chromosome numbers were obtained for *S. tentaculatum* (living plant number H.AR.042) and *S. hirsutum* (H.AR.036) from individuals cultivated by the third author in the botanical garden of Wageningen. Offspring of these accessions are now (2009) in cultivation at the Munich Botanical Garden. Each count is based on 10 to 15 nuclei from one individual. To obtain good-quality chromosomal spreads, root tip meristems were collected in the morning, pretreated for 3–5 hours with colchicine at 4°C, fixed with ethanol-acetic acid (3 : 1), and stored at –20°C until use. For basic karyotype assessment, hydrolyzed meristems were stained with Schiff's reagent, squashed under a cover slip, analyzed under a light microscope, and documented using a digital image capture system.

■ RESULTS

Phylogeny. — The combined sequence matrix (4319 characters, 98 accessions; Table 1) yielded a well-supported Areae clade in which all genera with more than one species were monophyletic, except for *Typhonium*, which split into three well-supported clades (Fig. 1). The largest of these, sister to the remaining genera, contains 31 of the 52 sampled species of *Typhonium*, including the type *T. trilobatum*. The second '*Typhonium*' clade includes only Australian endemics (Fig. 1); we refer to this clade as the Australian clade. Within the Australian clade, there are two statistically supported subclades, one containing *T. alismifolium*, *T. wilbertii* and *T. angustilobium* (the latter not monophyletic), and one containing *T. nudibaccatum*, *T. praetermissum* and the undescribed species *T.* sp. Kununurra, *T.* sp. Prince Regent and *T.* sp. Morgan River. The phylogenetic positions of other Australian taxa are not well resolved. The next-branching clade is *Theriophonum*, followed by the third '*Typhonium*' clade, which includes all species at one time placed in, or morphologically similar to, *Sauromatum* (Fig. 1). Within *Sauromatum*, there are three statistically supported clades, one of *S. hirsutum* and *S. tentaculatum*, one of *S. brevipes* and *S. venosum*, and one comprising *S. diversifolium*, *S. gaoligongense*, and *S. horsfieldii*. The sister relationship between the latter two is also well supported. The entire *Sauromatum* clade is sister to a well-supported clade of the remaining five genera of Areae, which are centered in the Mediterranean region.

Chromosome numbers. — For *Sauromatum*, we obtained new counts of $2n = 26$ for *S. hirsutum* and *S. tentaculatum*. Together with the other counts available for the genus (Fig. 2 and Discussion), a base number of $x = 13$ can be inferred, under the assumption that higher numbers in the genus are tetraploid or octoploid.

Table 1. Sizes of the individual and combined chloroplast and nuclear data matrices.

	Aligned nucleotides			Accessions		
DNA locus	Total	Excluded	Included	Total	Ingroup	Outgroup
trnK	2719	169	**2550**	**94**	92	2
rpl20-rps12	872	122	**750**	**58**	56	2
PhyC	1192	173	**1019**	**51**	49	2
Combined data			**4319**	**98**	96	2

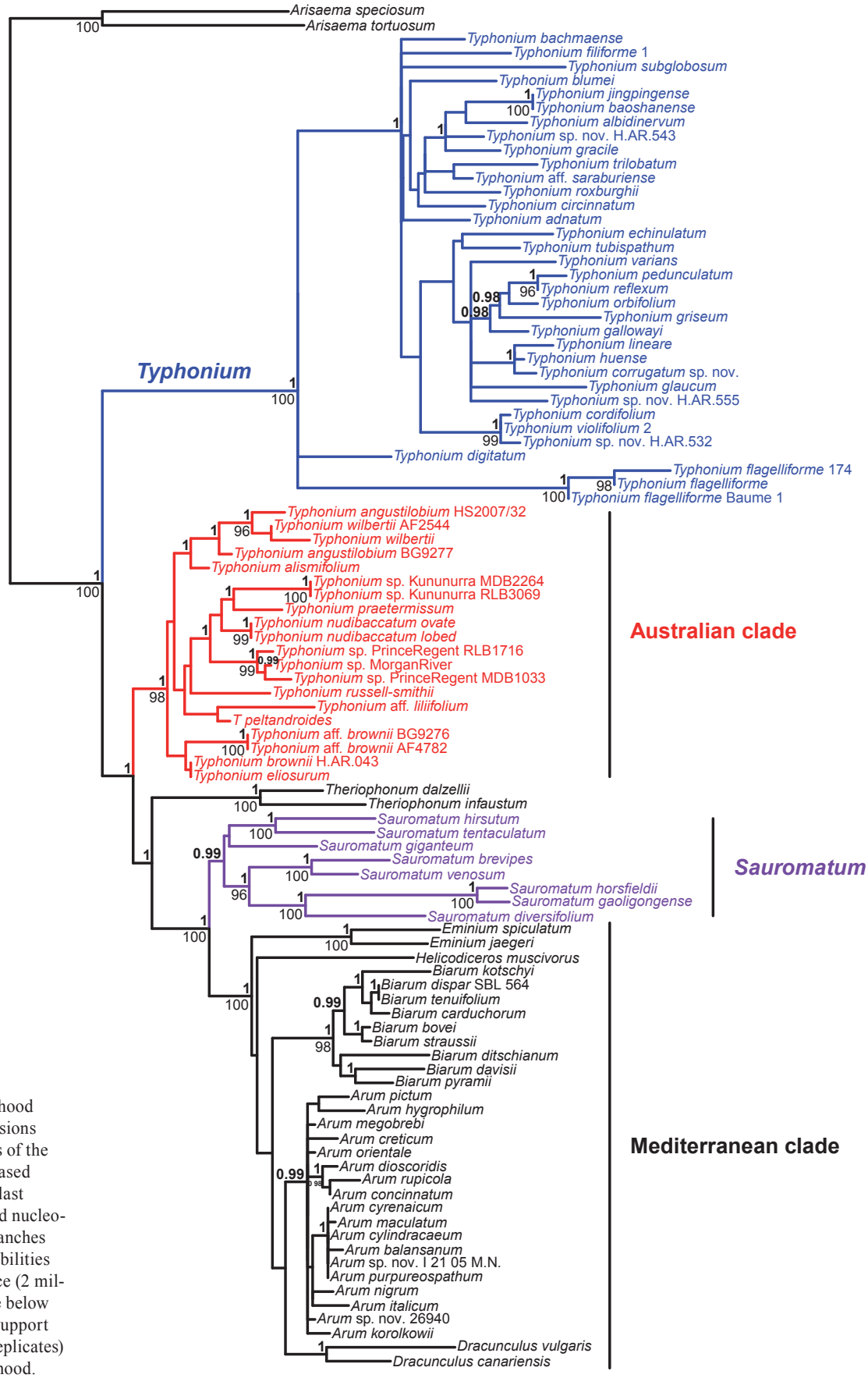

Fig. 1. Maximum likelihood phylogeny for 96 accessions representing 86 species of the nine genera of Areae based on nuclear and chloroplast sequences (4319 aligned nucleotides). Values above branches refer to posterior probabilities from Bayesian inference (2 million generations), those below branches to bootstrap support (percentages of 1000 replicates) under maximum likelihood.

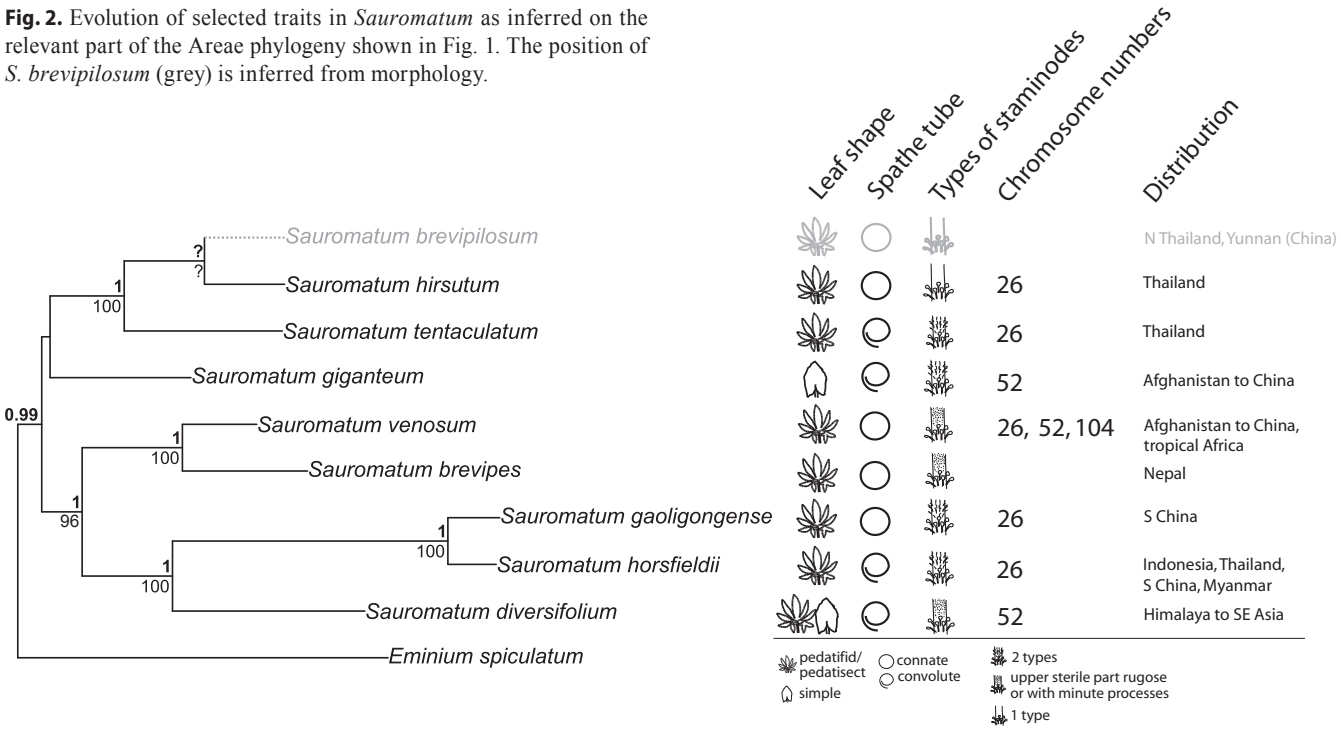

Fig. 2. Evolution of selected traits in *Sauromatum* as inferred on the relevant part of the Areae phylogeny shown in Fig. 1. The position of *S. brevipilosum* (grey) is inferred from morphology.

■ DISCUSSION

Phylogeny. — This study elucidates the phylogenetic relationships of *Typhonium* based on nuclear and chloroplast sequence data obtained for 86 of the 153 species of Areae. The results show that *Typhonium* splits into three clades that are not closely related. Fortunately, the type, *Typhonium trilobatum* (L.) Schott, falls into the largest clade so that only a small number of names need to be transferred to achieve monophyletic genera (see Taxonomic Conclusions).

The Australian species all fall in a clade (Fig. 1) except for *T. flagelliforme*, which also occurs in India and SE Asia (*T. blumei and T. roxburghii* are introduced to Australia). The arrival of *T. flagelliforme* in Australia appears to be quite recent, whereas the clade of endemic Australian species is a more ancient lineage that has diversified within Australia. This clade will need to be accorded genus rank to achieve a balanced classification of the tribe, and if *Lazarum mirabile* A. Hay (*Typhonium mirabile* (A. Hay) A. Hay) turns out to belong to this clade, *Lazarum* will become the correct name for this ninth genus of Areae. A revised morphological definition of *Lazarum* will be necessary, because the characters initially used to define *Lazarum* (Hay, 1992), viz., the connate spathe base, marcescent spathe (meaning that the withered spathe persists on the plant), annular septum at the spathe constriction, and shoot architecture are shared in only three species, *T. mirabile*, *T. praetermissum*, and *T. taylori* (Hay, 1997). An undescribed species with some of these characters is *T.* sp. Kununurra, which however lacks the annular septum. *Typhonium praetermissum* and *T.* sp. Kununurra are deeply nested within the Australian clade (Fig. 1), suggesting that these characters evolved independently within the Australian clade, rather than indicating a relationship with other genera, such as *Sauromatum*, as initially suggested by Hay (1992). Another six Australian species currently placed in *Typhonium*, viz., *T. cochleare* A. Hay, *T. johnsonianum* A. Hay & S.M. Taylor, *T. jonesii* A. Hay, *T. mirabile*, *T. taylorii* A. Hay, and *T. weipanum* A. Hay, remain to be sequenced.

Within the Australian clade, species with marcescent spathe bases were recovered as a monophyletic group with statistical support (*T.* sp. Kununurra, *T. praetermissum*, *T. nudibaccatum*, *T.* sp. Prince Regent, and *T.* sp. Morgan River). This clade is nearly equivalent to the 'nudibaccati group' of Hay (1993), with the inclusion of several species discovered since that publication (Hay 1997). The expanded 'nudibaccati group' is restricted to the Kimberley region of West Australia and the northern part of the Northern Territory. The remainder of the Australian species falls into several groups showing geographic structuring, with variable levels of support. A strongly supported clade containing *T. angustilobium*, *T. wilbertii* and *T. alismifolium* appears restricted to tropical Queensland. Specimens from the Northern Territory previously assigned to *T. angustilobium* requires molecular confirmation of its identity, but could not be sampled for this study. Collections from central arid Australia attributed to *T. alismifolium* in Hay (1993) belong to an undescribed species.

Typhonium peltandroides and *T.* aff. *liliifolium* are sister taxa in Fig. 1, but without strong support. Both species occur in the Kimberley region of Western Australia and may be related to *T. liliifolium* s.str. from the Northern Territory because all three species share entire leaves with dense venation. *Typhonium eliosurum*, *T. browni* and *T.* aff. *brownii* also form a clade in Fig. 1, albeit without support. These species are distributed along the east coast of Australia and share laterally elongated rather than depressed-globose corms as found in most other Australian taxa.

The newly revealed *Sauromatum* clade includes six species that were at one time placed in, or thought similar to, *Sauromatum*. Only *S. diversifolium* and *S. tentaculatum* were never before compared to *Sauromatum*, but their morphology fits the genus well (below). Additionally, both species have a chromosome number based on $x = 13$, which appears to be the base number of *Sauromatum*, a characteristic of the genus first reported here.

Sauromatum can be separated from all other Areae genera by a combination of four characters (Fig. 2; Fig. 3 shows the inflorescences of all nine species of *Sauromatum*): *Sauromatum* has (1) pedatisect leaves; (2) a spathe tube with fused margins, (3) clavate lower staminodes; and (iv) upper staminodes that are differently shaped from the lower ones and/or longitudinal ridges on the spadix between the lower staminodes and the stamens. The ridges on the spadix may represent vestigial staminode bases, as is visible in *S. giganteum* (Fig. 3C). When the last two of these four characters apply and a species has pedatisect leaves and/or a fused spathe tube, then it can be assigned to *Sauromatum*. On these morphological grounds, we here also transfer *T. brevipilosum* (as yet unsequenced) to *Sauromatum*. Two other species that Sriboonma & al. (1994) revealed as closely related to the investigated *Sauromatum* species are *T. omeiense* H. Li and *T. alpinum* C.Y. Wu ex H. Li, Y. Shiao & S.L. Tseng. However, these names will be synonymized with, respectively, *S. horsfieldii* and *S. diversifolium* in a forthcoming treatment for the *Flora of China* (of which WH is a coauthor).

As here circumscribed, *Sauromatum* has 5–13-foliolate pedatisect leaves, except for *S. giganteum* and some forms of *S. diversifolium*, which have simple leaves. *Sauromatum brevipes*, *S. brevipilosum*, *S. hirsutum*, *S. gaoligongense* and *S. venosum* have a spathe tube with fused margins. This character is never found in *Typhonium* (s.str.) but occurs in its sister clade (Fig. 1), namely in *Biarum*, *Eminium jaegeri*, *T. mirabile*, *T. taylori*, *T. praetermissum*, and the undescribed *T.* sp. Kununurra. The only species of *Typhonium* s.str. that has two types of staminodes is *T. flagelliforme* (Fig. 3J), but here the lower ones are not clavate, nor are the leaves pedatisect or the spathe tube fused.

The phylogenetic relationships shown here (Figs. 1–2) suggest that the fused spathe tube has evolved three times independently in *Sauromatum* (once in *S. hirsutum/S. brevipilosum*, once in *S. venosum/S. brevipes*, and once in *S. gaoligongense*). In contrast, the clavate-shaped lower staminodes seem to have evolved once, along with the distinct upper staminodes (Fig. 3A–B), later reduced to varying extents (Fig. 3C–I). If *S. brevipilosum* is indeed the sister of *S. hirsutum* (Fig. 2), the complete loss of the upper staminodes happened once, their reduction twice (in *S. venosum/S. brevipes* and *S. diversifolium*). The pedatisect leaves seem to be the plesiomorphic condition in the genus that has been lost twice (in *S. giganteum* and *S. diversifolium*).

Chromosome numbers in *Typhonium*, *Sauromatum*, and the Australian clade. — In *Sauromatum* chromosome numbers are available for *S. horsfieldii* ($2n = 26$), *S. diversifolium*, *S. giganteum* ($2n = 52$), *S. venosum* ($2n = 26$, 52, 104; Petersen, 1989; Bogner & Petersen, 2007), and *S. gaoligongense* ($2n = 26$; Li Heng, Kunming Institute of Botany, pers. comm. on 20 July 2009). Hence, including our new counts for *S. hirsutum* and *S. tentaculatum* of $2n = 26$, the base chromosome number of *Sauromatum* is $x = 13$. From these counts, the two most widespread species, *S. giganteum* (Afghanistan to China) and *S. venosum* (Afghanistan to China, Africa) appear to be tetraploid,

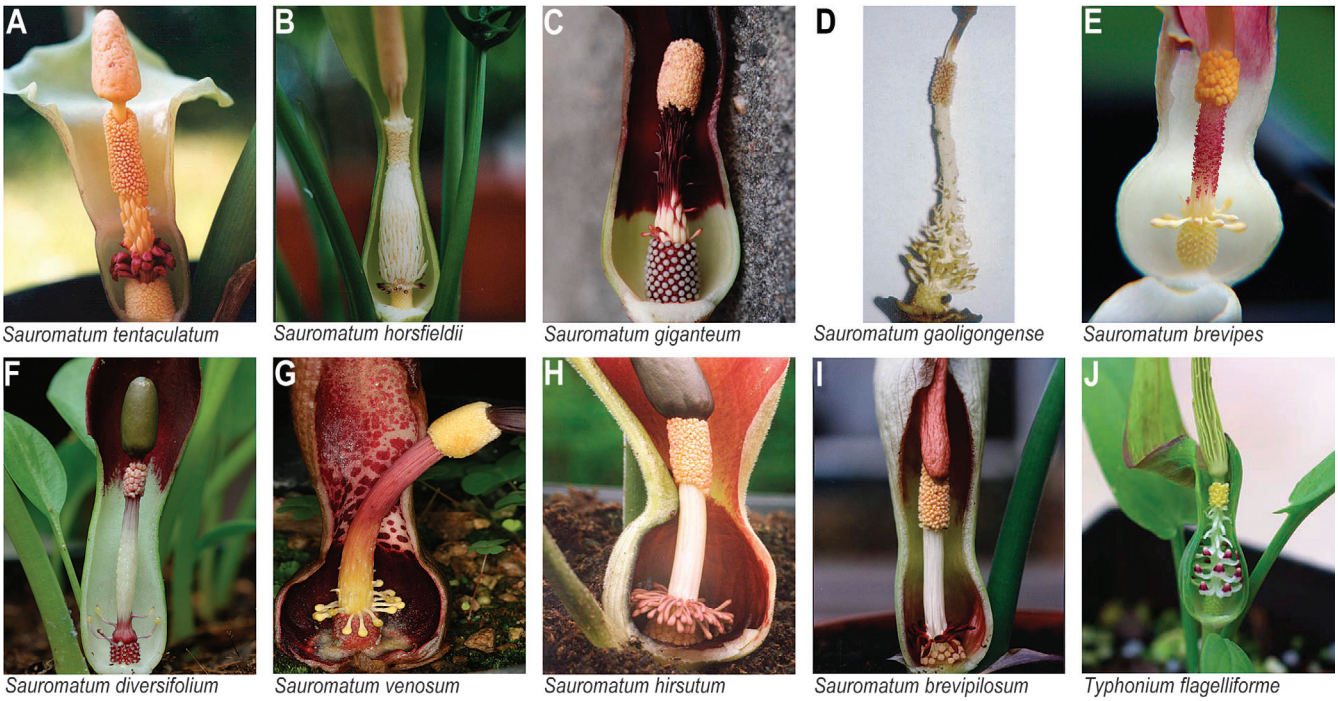

Fig. 3. Longitudinally opened spathes of the nine species of *Sauromatum* **(A–I)** and of *T. flagelliforme* **(J)**, showing the different types of staminodes. Photos A–C, E–F, and H–J by W. Hetterscheid from plants cultivated in his greenhouse; photo D by H. Li, Kunming Institute of Botany; photo E by Arno Clement; photo G by B.O. Schlumpberger, Systematic Botany, University of Munich.

and *S. venosum* appears to comprise also diploid, and octoploid forms. The five remaining, more narrowly distributed species all appear to be diploid. The switch to polyploidy appears to have happened three times, but chromosome numbers are still lacking for two species (*S. brevipilosum* and *S. brevipes*).

In *Typhonium*, by contrast, chromosome numbers are extremely variable: the early-diverging *T. flagelliforme* has $2n = 16$, while other species have $x = 5, 7, 8, 9, 10$ or 13 and most probably also $x = 4, 6, 11$ (N. Cusimano, unpub. data). Diploid chromosome numbers range from $2n = 8$ to $2n = 78$. Aneuploidization and subsequent polyploidization events (or vice versa), or other complex chromosome rearrangements, seem to have played an important role in the evolution of *Typhonium*, leading to the existing variety of chromosome numbers. The drastic reduction of chromosome number could have happened through chromosome fusion, translocations of chromosome parts and/or loss of DNA.

For the Australian clade, only two chromosome numbers have been reported, both extremely high: *T. eliosurum* ($2n >$ 100) and *T. brownii* ($2n = 160$; Briggs in Evans, 1961). Along with an undescribed species from New South Wales, these species may belong to a polyploid complex.

■ TAXONOMIC CONCLUSIONS

Our results show that the broadly circumscribed *Typhonium* of Hetterscheid & Boyce (2000) is polyphyletic and comprises three distinct clades, which should be recognized at generic rank to achieve a balanced classification of the Areae. The Asian and Malesian species form a clade (*Typhonium* s.str.) that is sister to the other genera of Areae. The Australian species of *Typhonium* so far sequenced form a distinct clade. *Theriophonum*, from southern India, diverges next, followed by *Sauromatum*, now composed of nine species, and sister to a clade including the Mediterranean genera of Areae (*Arum*, *Biarum*, *Dracunculus*, *Eminium*, *Helicodiceros*). The genus *Sauromatum* can be circumscribed not only genetically, but also morphologically as we have shown here. Application of the name *Lazarum* for the Australian clade (Fig. 1) awaits the sequencing of the type of this generic name. At this stage, therefore, *Typhonium* s.str. and the Australian clade are not defined morphologically, but on our molecular evidence are clearly distinct.

In the following, we resurrect the genus *Sauromatum*, make the necessary five new combinations, and present a key to the nine species of *Sauromatum*. Detailed descriptions of all species and up-to-date information on their geographic distribution are available elsewhere (Sriboonma & al., 1994; Wang & Li, 1999; Hetterscheid & Boyce, 2000; Hetterscheid & al., 2001).

Sauromatum Schott in Schott & Endlicher, Melet. Bot.: 17. 1832 – Lectotype (designated in Taxon 16: 518. 1967): *S. guttatum* Schott (*Arum guttatum* Wallich 1831, non Salisbury 1796).

Sauromatum brevipes (Hook. f.) N.E. Brown in Gard. Chron., ser. 3, 34(2): 93. 1903 ≡ *Typhonium brevipes* Hook. f. in Fl. Brit. India 6: 511. 1893 – Syntypes: Darjeeling, 7500 ft., *Clarke 26708* (K); Jore Pokri, 7600 ft., *Gammie s.n.* (K).

Sauromatum gaoligongense Z.L. Wang & H. Li in Acta Bot. Yunnan., suppl. 11: 61. 1999 ≡ *Typhonium gaoligongense* (Z.L. Wang & H. Li) Hett. & P.C. Boyce in Aroideana 23: 51. 2000 – Holotype: China, Yunnan prov., Baoshan Xianm, *Li Heng & G. Ruckert 11309A* (KUN).

Sauromatum horsfieldii Miq. in Fl. Ned. Ind. 3: 196. 1855 ≡ *Typhonium horsfieldii* (Miq.) Steenis in Bull. Jard. Bot. Buitenzorg, ser. 3, 17: 403. 1948 – Holotype: Java, Oenagaran, *Horsefield s.n.* (K). [For full synonymy see Sriboonma & al., 1994.]

Sauromatum venosum (Dryand. ex Ait.) Kunth in Enum. Pl. 3: 28. 1841 ≡ *Arum venosum* Dryand. ex Ait. in Hort. Kew. 3: 315. 1789 ≡ *Desmesia venosum* (Dryand. ex Ait.) Raf. in Fl. Tellur. 3: 63. 1837 ≡ *Sauromatum guttatum* (Ait.) Schott var. *venosum* (Ait.) Engl. in Pflanzenr. IV 23F (Heft 73): 125. 1920 ≡ *Typhonium venosum* (Dryand. ex Ait.) Hett. & P.C. Boyce in Aroideana 23: 51. 2000 – Holotype: Plant of unknown origin introduced into cultivation at Kew by William Malcolm in 1774 (BM). [For full synonymy see Hetterscheid and Boyce, 2000.]

Sauromatum brevipilosum (Hett. & M. Sizemore) Cusimano & Hett., **comb. nov.** ≡ *Typhonium brevipilosum* Hett. & M. Sizemore in Aroideana 23: 52. 2000 – Holotype: Indonesia, Sumatera, West Sumatera, near Aeksah, *Hetterscheid H.AR.097-T* (orig. coll. *Sizemore s.n.*) flowered in cult. in Leiden Bot. Gard., 29 Nov 1999 (L, spirit coll.).

Sauromatum diversifolium (Wall. ex Schott) Cusimano & Hett., **comb. nov.** ≡ *Typhonium diversifolium* Wall. [in Wallich's Numer. List n. 8933. 1949, nom. nud.] ex Schott in Aroideae 13: 20. 1855 ≡ *Heterostalis diversifolia* Schott in Oesterr. Bot. Wochenbl. 7: 267. 1857 – Holotype: Nepal, Wallich's Numer. List. no. 8933a in 1821 (K). [For full synonymy see Sriboonma & al., 1994.]

Sauromatum giganteum (Engl.) Cusimano & Hett. **comb. nov**. ≡ *Typhonium giganteum* Engl. in Bot. Jahrb. Syst. 4: 66. 1883 – Holotype: China, Beijing, *Skatschkow s.n.* (LE). [For full synonymy see Sriboonma & al., 1994.]

Sauromatum hirsutum (S.Y. Hu) Cusimano & Hett., **comb. nov**. ≡ *Arisaema hirsutum* S.Y. Hu in Dansk Bot. Ark. 23(4): 454. 1968 ≡ *Typhonium hirsutum* (S.Y. Hu) J. Murata & Mayo in Kew Bull. 46(1): 129. 1991 – Holotype: Thailand, *Payap 3939* (C).

Sauromatum tentaculatum (Hett.) Cusimano & Hett., **comb. nov.** ≡ *Typhonium tentaculatum* Hett. in Aroideana 24: 49. 2001 – Holotype: Thailand SW 37, Kanchanaburi, Sangklaburi Distr., Lai Wo Subdistr., Toong Yai Wildlife Reserve, Ban Saneh Pawng, West side of Paneh limestone mountain, 300 m *Hetterscheid H.AR.042-T* (orig. coll. *J.F. Maxwell 93-647*), flowered in cult. in the Leiden Bot. Gard. 9 Apr 1997 (BKF, spirit coll.).

Key to *Sauromatum* species

1 Two types of staminodes, upper clearly of different shape or reduced compared to the lower ones 2
1 Only one type of staminodes, upper sterile part longitudinally grooved and roughened with projections or processes, or naked. 5
2 Spathe tube fused; 3–5 bulbils in the lower part of the petiole . . . . . ***S. gaoligongense***
2 Spathe tube convolute. 3
3 Lower staminodes clearly clavate. 4
3 Lower staminodes clavate/spathulate, clavate part anvil shaped or dorso-ventrally flattened, dark purple; upper staminodes narrowly spindle shaped, whitish . . . . . ***S. tentaculatum***
4 Leaves simple, ovate, cordate to hastate; upper staminodes smaller than the lower ones, subulate or occasionally absent . . . . . ***S. giganteum***
3 Leaves pedatisect; upper staminodes filiform, gradually shorter towards the male zone . . . . . ***S. horsfieldii***
5 Spathe tube free; leaf blade simple and ovate-lanceolate, cuneate to hastate 3–5-lobed or 5–9-foliolate pedatisect; upper sterile part of the spadix naked or with apiculate projections. . . . . ***S. diversifolium***
5 Spathe tube fused, at least basal part 6
6 Petiole and leaf blade with hairs; upper sterile part of the spadix axis completely naked. 7
6 Petiole and leaf blade without hairs, upper sterile part of the spadix axis rough, shaggy or with minute processes (highly reduced staminodes) 8
7 Hairs distinct and long; also outside surface of spathe covered with hairs . . . . . ***S. hirsutum***
7 Hairs short (ca 0.5 mm); outside surface of spathe smooth. . . . . ***S. brevipilosum***
8 Leaflets oblong-lanceolate, apex acuminate; inflorescence up to 40 cm long; spathe tube dark purple inside, spathe blade inside maculate . . . . . ***S. venosum***
8 Leaflets linear-lanceolate, apex long acuminate; lower clavate staminodes white, upper minute processes purple; inflorescence max. 7.5 cm long; spathe tube inside greenish to white, spathe blade inside not maculate, dull purple basally and pink above . . . . . ***S. brevipes***

■ ACKNOWLEDGEMENTS

For plant material, we thank Josef Bogner, Li Heng, Clare Herscovitch, Wolfram Lobin and Allan Galloway. We also thank Josef Bogner and two anonymous reviewers for their comments. This study was supported by DFG grant RE 603/7-1.

■ LITERATURE CITED

Bogner, J. & Boyce, P.C. 2008. *Eminium jaegeri* (Araceae), a new species from northwestern Iran. *Willdenowia* 38: 149–153.
Bogner, J. & Petersen, G. 2007. The chromsome numbers of the aroid genera. *Aroideana* 30: 82–90.
Boyce, P.C. 1993. *The genus* Arum. Kew: The Bentham-Moxon Trust, Royal Botanic Gardens, Kew.
Boyce, P.C. 2006. *Arum*: A decade of change. *Aroideana* 29: 132–137.
Boyce, P.C. 2008. A monograph of the genus *Biarum*—special part. *Curtis's Bot. Mag.* 25: 1–119.
Brown, N.E. 1903. New or noteworthy plants – *Sauromatum brevipes*. *Gard. Chron*, ser. 3, 34: 93–94.
Dao, Z.L., Chen, S.-T., Ji, Y.-H. & Li, H. 2007. *Typhonium baoshanense* Z.L. Dao & H. Li: A new species of Araceae from western Yunnan, China. *Acta Phytotax. Sin*. 45: 234–238.
Evans, O. 1961. Araceae. *Contr. New South Wales Natl. Herb., Fl. Ser.* 21/22: 6–13.
French, J.C., Chung, M.G. & Hur, Y.K. 1995. Chloroplast DNA phylogeny of the Ariflorae. Pp. 255–275 in: Rudall, P.J., Cribb, P., Cutler, D.F. & Humphries, C.J. (eds.), *Monocotyledons: Systematics and evolution*. Kew: Royal Botanic Gardens.
Hay, A. 1992. A new Australian genus of Araceae, with notes on generic limits and biogeography of the Areae. *Bot. J. Linn. Soc.* 109: 427–434.
Hay, A. 1993. The genus *Typhonium* (Araceae–Areae) in Australasia. *Blumea* 37: 345–376.
Hay, A. 1997. Two new species and a new combination in Australian *Typhonium* (Araceae tribe Areae). *Edinburgh J. Bot.* 54: 329–336.
Hay, A. & Taylor, S.M. 1996. A new species of *Typhonium* Schott (Araceae–Areae) from the Northern Territory, with notes on the conservation status of two Areae endemic to the Tiwi Islands. *Telopea* 6: 563–568.
Hetterscheid, W.L.A. & Boyce, P.C. 2000. A reclassification of *Sauromatum* Schott and new species of *Typhonium* Schott (Araceae). *Aroideana* 23: 48–55.
Hetterscheid, W.L.A. & Galloway, A. 2006. New *Typhonium* (Araceae) species from Thailand. *Aroideana* 29: 80–85.
Hetterscheid, W.L.A. & Nguyen, V.D. 2001. Three new species of *Typhonium* (Araceae) from Vietnam. *Aroideana* 24: 24–29.
Hetterscheid, W.L.A., Sookchaloem, D. & Murata, J. 2001. *Typhonium* (Araceae) of Thailand: New species and a revised key. *Aroideana* 24: 30–55.
Hooker, J.D. 1893. *Flora of British India*, vol. 6, *Orchideae to Cyperaceae*. London: Reeve.
Hu, S.Y. 1968. Araceae. Studies in the Flora of Thailand 41. *Dansk Bot. Ark.* 23: 411–457.
Huelsenbeck, J.P. & Ronquist, F. 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.
Johnson, L.A. & Soltis, D.E. 1994. *MatK* DNA sequences and phylogenetic reconstruction in Saxifragaceae s.str. *Syst. Bot.* 19: 143–156.
Kunth, C.S. 1841. *Enumeratio plantarum*, vol. 3. Stuttgart: Cottae.
Lobin, W., Neumann, M., Bogner, J. & Boyce, P.C. 2007. A new *Arum* species (Areae, Araceae) from NE Turkey and Georgia. *Willdenowia* 37: 445–449.
Maddison, W.P. & Maddison, D.R. 1992. *MacClade: Analysis of phylogeny and character evolution*, version 3.0. Sunderland, Massachusetts: Sinauer.
Mayo, S.J., Bogner, J. & Boyce, P.C. 1997. *The genera of Araceae*. Kew: The Trustees, Royal Botanic Gardens.
Miquel, F.A.W. 1855. *Flora van Nederlandsch Indie*, vol. 3. Amsterdam: C.G. van der Post.
Miquel, F.A.W. 1864. Mantissa Araliacearum, Ericacearum, Cupuliferarum et Aracearum. *Ann. Mus. Bot. Lugduno-Batavi* 1: 219–221.
Murata, J. & Mayo, S.J. 1991. A new combination in *Typhonium* (Araceae). *Kew Bull.* 46: 129–131.
Murata, J., Sookchaloem, D. & Hetterscheid, W.L.A. 2002. *Typhonium watanabei* (Araceae), a new species from Thailand. *J. Jap. Bot.* 77: 163–166.
Nguyen, V.D. 2008. *Typhonium stigmatilobatum* (Araceae tribe Areae), a new species from Vietnam. *Kew Bull.* 63: 491–493.
Petersen, G. 1989. Cytology and systematics of Araceae. *Nord. J. Bot.* 9: 119–166.

Rambaut, A. & Drummond, A.J. 2007. Tracer, version 1.4. Available from http://beast.bio.ed.ac.uk/Tracer.

Renner, S.S. & Zhang, L.-B. 2004. Biogeography of the *Pistia* clade (Araceae): Based on chloroplast and mitochondrial DNA sequences and Bayesian divergence time inference. *Syst. Biol.* 53: 422–432.

Ronquist, F. & Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.

Schott, H.W. 1832. Araceae. Pp. 16–22 in: Schott, H.W. & Endlicher, S. (eds.), *Meletemata botanica*. Vienna: Gerold.

Sivadasan, M. & Nicolson, D.H. 1982. A revision of *Theriophonum* (Araceae). *Kew Bull.* 37: 277–290.

Sookchaloem, D. & Murata, J. 1997. A new species of *Typhonium* from Thailand. *Thai Forest Bull., Bot.* 25: 57–59.

Sriboonma, D., Hasebe, M., Murakami, N., Murata, J. & Iwatsuki, K. 1993. Phylogeny of *Typhonium* (Araceae) inferred from restriction fragment analysis of chloroplast DNA. *J. Pl. Res.* 106: 11–14.

Sriboonma, D., Murata, J. & Iwatsuki, K. 1994. A revision of *Typhonium* (Araceae). *J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot.* 14: 255–313.

Stamatakis, A., Hoover, P. & Rougemont, J. 2008. A rapid bootstrap algorithm for the RAxML web-servers. *Syst. Biol.* 57: 758–771.

Van Steenis, C.G.G.J. 1948. Miscellaneous botanical notes I. *Bull. Jard. Bot. Buitenzorg*, ser. 3, 17: 383–411.

Wang, Z.-L. & Li., H. 1999. *Sauromatum gaoligongense* (Araceae), a new species from Gaoling mountains. *Acta Bot. Yunnan., Suppl.* 11: 61–64.

Wang, Z.-L., Li, H. & Bian, F. 2002. *Typhonium jinpingense*, a new species from Yunnan, China, with the lowest diploid chromosome number in Araceae. *Novon* 12: 286–289.

Appendix. Voucher information for studied species. GenBank numbers are given for the three markers sequenced, *trnK*, *PhyC* and *rpl20-rps12*; an n-dash denotes a missing marker.

Outgroups: *Arisaema speciosum* (Wall.) Mart., *Hetterscheid H.AR.294* (L, spirit coll.), EU886502, EU886470, AY279168; *Arisaema tortuosum* (Wall.) Schott, *Anaimudi 20/5*, EU886577, EU886469, AY248920; ***Arum*** L.: *A. balansanum* R. Mill, *V. Haller & M. Koenen 1*91*TR H*K* (BONN), EU886512, –, EU886624; *A. concinnatum* Schott, *B.W. Magrys s.n.*, cult. 15. Mar. 02, EU886516, –, GU255991; *A. creticum* Boiss. & Heldr., *Tillich 4881* (M), EU886504, –, EU886595; *A. cyrenaicum* Hruby, LY-0-BONN-6425 (BG Bonn), EU886515, –, EU886623; *A. dioscoridis* Sibth. & Sm., B. W. Magrys s.n., cult. 15. Mar. 02, EU886505, –, GU255992; *A. hygrophilum* Boiss., CY-0-BONN-6427 (BG Bonn), EU886509, EU886471, EU886620; *A. italicum* Mill., BG Mainz, cult. 20 Jul 2001, EU886517, EU886472, AY248922; *A. korolkowii* Regel, *S. Volz 20* (M), EU886589, –, EU886598; *A. maculatum* L., *Cusimano06–3* (M), EU886506, –, EU886593; *A. megobrebi* Lobin, *M. Neumann & al. 24219* (BONN), EU886513, –, EU886625; *A. nigrum* Schott, *Cusimano06–1* (M), EU886507, EU886473, EU886597; *A. orientale* Bieb., *A. Groeger 06/1845w*, EU886510, –, EU886621; *A. pictum* L. f., xx-0-BONN-273 (BG Bonn), EU886518, –, EU886596; *A. purpureospathum* Boyce, Tuber from E. Walton, 15 Apr 2002, EU886508, –, EU886594; *A. rupicola* Boiss., *J. Bogner 1790* (M), EU886519, –, EU886592; *A.* sp. nov., *M. Neumann I 21 05 M.N.*, EU886514, –, EU886622; *A.* sp. nov., *W. Lobin 26940* (BONN), EU886511, –, EU886626; ***Biarum*** Schott: *B. bovei* Blume, *T.F. Hewer H7951* (M), EU886529, –, EU886601; *B. carduchorum* (Schott) Engl., *M. Jaeger JLMS-60* (BG Giessen), EU886521, EU886478, EU886618; *B. davisii* Turrill, MO living acc. 78231, EU886525, EU886479, AY248923; *B. dispar* (Schott) Talavera, *M. Jaeger SBL 564* (BG Giessen), EU886522, –, EU886619; *B. ditschianum* Bogner & Boyce, BG Bonn 4695, rec., EU886526, EU886477, EU886600; *B. kotschyi* (Schott) B. Mathew ex H. Riedl, TR-0-BONN-8431 (BG Bonn), EU886527, –, EU886599; *B. pyramii* (Schott) Engler, *J. Mayr s.n.* (BG Giessen), EU886523, –, EU886617; *B. straussii* Engler, *M. Jaeger JZZ-54* (BG Giessen), EU886524, –, EU886615; *B. tenuifolium* (L.) Schott, ES-0-BONN-16014 (BG Bonn), EU886528, –, AY248924; ***Dracunculus*** P. Miller: *D. canariensis* Kunth, ES-0-BONN-13049 (BG Bonn), EU886531, EU886475, AY248926; *D. vulgaris* Schott, *T. Croat 78286* (MO), EU886532, EU886476, AY248927; ***Eminium*** (Blume) Schott: *E. jaegeri* Bogner & P.C. Boyce, *M. Jaeger JJMZ-67a* (M), EU886520, –, EU886616; *E. spiculatum* (Blume) Schott, *M. Neumann 27/96* (BONN), EU886530, EU886474, AY248928; ***Helicodiceros*** Schott: *Helicodiceros muscivorus* (L. f.) Engl., MO living acc. 71821, EU886533, EU886480, AY248929; ***Sauromatum*** Schott: *S. brevipes* (Hook. f.) N.E. Brown, J. McClements cult., EU886539, EU886484, EU886608; *S. diversifolium* (Wall.) Cusimano & Hett., *Hetterscheid H.AR.484* (L, spirit coll.), EU886540, EU886482, EU886605; *S. gaoligongense* Wang & H. Li, *Chen YM 024* (KUN), EU886590, EU886487, –; *S. giganteum* (Engl.) Cusimano & Hett., J.W. Waddick cult., 20 Aug. 2001, EU886536, EU886490, AY248938; *S. hirsutum* (S.Y. Hu) Cusimano & Hett., *Hetterscheid H.AR.036* (L, spirit coll.), EU886542, EU886489, AY248939; *S. horsfieldii* Miq., *J. Murata 3* (TI), EU886541, EU886483, EU886604; *S. tentaculatum* (Hett.) Cusimano & Hett., *Hetterscheid H.AR.042* (L, spirit coll.), EU886543, EU886488, EU886612; *S. venosum* (Dryand. ex Ait.) Kunth, *J. Bogner s.n.* (M), 27. Jun. 02, EU886544, EU886481, EU886603; ***Theriophonum*** Blume: *T. dalzelii* Schott, *J. Murata s.n.*, 21 Aug. 2002, –, –, AY248936; *T. dalzelii*, *P. Bruggemann PB 168*, cult., EU886534, EU886486, –; *T. infaustum* N.E. Br., *P. Bruggemann PB 099*, cult., EU886535, EU886485, EU886602; ***Typhonium*** Schott: *T.* adnatum Hett. & Sookchaloem, *A. Galloway AGA-1095-17*, EU886547, –, –; *T. albidinervum* C.Z. Tang & H. Li, *J. Murata 1* (TI), EU886548, EU886497, AY248937; *T. bachmaense* Nguyen Van Dzu & Hett., *Nguyen Van Dzu 185* (HN), EU886549, –, –; *T. baoshanense* Z.L. Dao & H. Li, *Chen YM 017* (KUN), EU886591, –, EU886629; *T. blumei* Nocolson & Sivadasan, *G. Hausner 5* (M), EU886553, –, –; *T. circinnatum* Hett. & J. Mood, *Hetterscheid H.AR.258* (L, spirit coll.), EU886551, –, –; *T. corrugatum* sp. nov, *Bogner 2962* (M), GU255984, –, –; *T. digitatum* Hett. & Sookchaloem, *Hetterscheid H.AR.215* (L, spirit coll.), EU886552, –, –; *T. echinulatum* Hett. & Sookchaloem, *Hetterscheid H.AR.225* (L, spirit coll.), EU886554, EU886499, –; *T. filiforme* Ridl., *Hetterscheid H.AR.128* (L, spirit coll.), EU886555, –, –; *T. flagelliforme* (Lodd.) Blume, SE Asia, *Hetterscheid H.AR.028* (L, spirit coll.), EU886556, –, –; *T. flagelliforme* (Lodd.) Blume, Cape York, QLD, Australia, *Baume 1* (CNS), –, GU255955, –; *T. flagelliforme* (Lodd.) Blume, *Michel CR 2016* (DNA), GU255983, –, –; *T. gallowayi* Hett. & Sookchaloem, *A. Galloway AGA-0516-01*, EU886558, –, –; *T. glaucum* Hett. & Sookchaloem, *Hetterscheid H.AR.535* (L, spirit coll.), EU886559, –, –; *T. gracile* (Roxb.) Schott, *J. Murata 2* (TI), EU886563, EU886495, –; *T. griseum* Hett. & Sookchaloem, *Hetterscheid H.AR.044* (L, spirit coll.), EU886561, –, –; *T. huense* V.D. Nguyen & Croat, *Hetterscheid H.AR.178* (L, spirit coll.), EU886557, –, –; *T. jingpingense* Z.L. Wang, H. Li & F.H. Bian, *Chen YM 023* (KUN), EU886564, EU886498, EU886614; *T. lineare* Hett. & V.D. Nguyen, *Hetterscheid H.AR.244* (L, spirit coll.), EU886565, –, –; *T. orbifolium* Hett. & Sookchaloem, *Hetterscheid H.AR.227* (L, spirit coll.), EU886566, –, –; *T. pedunculatum* Hett. & Sookchaloem, *Hetterscheid H.AR.559* (L, spirit coll.), EU886567, –, –; *T. reflexum* Hett. & Sookchaloem, *A. Galloway AGA-1547-01*, EU886568, –, –; *T. roxburghii* Schott, *J.C. Wang 11621* (TNU), EU886569, –, EU886613; *T. saraburiense*? Sookchaloem, Hett. & Murata, *Hetterscheid H.AR.538* (L, spirit coll.), EU886570, –, –; *T.* sp. nov., *Hetterscheid H.AR.555* (L, spirit coll.), EU886550, –, –; *T.* sp. nov., *Hetterscheid H.AR.532* (L, spirit coll.), EU886572, –, –; *T.* sp. nov., *Hetterscheid H.AR.543* (L, spirit coll.), EU886573, –, –; *T. subglobosum* Hett. & Sookchaloem, *A. Galloway AGA-1006-01*, EU886546, –, –; *T. trilobatum* (L.) Schott, *J. Murata 5* (TI), EU886571, EU886496, AY248941; *T. tubispathum* Hett. & A.Galloway, *Hetterscheid H.AR.469* (L, spirit coll.), EU886574, –, –; *T. varians* Hett. & Sookchaloem, *Hetterscheid H.AR.560* (L, spirit coll.), EU886575, EU886494, –; *T. violifolium* Gagnep., *Hetterscheid H.AR.461* (L, spirit coll.), EU886560, –, –; *T. violifolium* 2 Gagnep., *Hetterscheid H.AR.168* (L, spirit coll.), EU886562, –, EU886611; **Australian *Typhonium* (*Lazarum*** A. Hay): *T. alismifolium* F. Muell. s.str., *B. Gray 9146* (CNS), GU255975, GU255961, –; *T. angustilobium* F. Muell., *B. Gray 9277* (CNS), GU255974, GU255960, –; *T. angustilobium* F. Muell., *H. Schaefer 2007/32* (M), EU886576, EU886491, EU886609; *T. brownii* Schott, *Hetterscheid H.AR.043* (L, spirit coll.), EU886538, EU886492, EU886607; *T. eliosurum* (F. Muell. ex Benth.) O.D. Evans, *Hetterscheid H.AR.364* (L, spirit coll.), EU886537, EU886493, EU886606; *T. nudibaccatum* A. Hay (linear), *R.L. Barrett 3957* (PERTH), GU255981, GU255968, –; *T. nudibaccatum* A. Hay (ovate), *R.L. Barrett 3957* (PERTH), –, GU255969, GU255990; *T. peltandroides* A. Hay, M.D. Barrett & R.L. Barrett, *M.D. Barrett 599* (PERTH), GU255973, GU255958, GU255986; *T. praetermissum* A. Hay, *Hay s.n.* 16.10.1996 (NSW), GU255982, GU255970, –; *T. russell-smithii* A. Hay, *I. Cowie 104311* (DNA), GU255985, –, –; *T.* sp. aff. *brownii* Schott, *B. Gray 9276* (CNS), GU255971, GU255956, –; *T.* sp. aff. *brownii* Schott, *A. Ford 4782* (CNS), GU255972, GU255957, –; *T.* sp. aff. *liliifolium* sp. Theda, *M.D. Barrett & R.L. Barrett MDB 1504* (PERTH), –, GU255959, GU255987; *T.* sp. Kununurra, *M.D. Barrett & R.L. Barrett MDB 2264* (PERTH), –, GU255965, –; *T.* sp. Kununurra, *R.L. Barrett 3069* (PERTH), GU255979, GU255966, GU255989; *T.* sp. Morgan River, *M.D. Barrett & R.L. Barrett MDB 2265* (PERTH), GU255980, GU255967, –; *T.* sp. Prince Regent, *R.L. Barrett & M.D. Barrett RLB 1716* (PERTH), GU255977, GU255963, GU255988; *T.* sp. Prince Regent, *M.D. Barrett 1033* (PERTH), GU255978, GU255964, –; *T. wilbertii* A. Hay, *A. Ford 2544* (CNS), GU255976, GU255962, –; *T. wilbertii* A. Hay, *Hetterscheid H.AR.033* (L, spirit coll.), EU886545, –, EU886610.