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Maximum likelihood inference implies a high, not a low, ancestral haploid chromosome number in Araceae, with a critique of the bias introduced by 'x'

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• *Background and Aims* For 84 years, botanists have relied on calculating the highest common factor for series of haploid chromosome numbers to arrive at a so-called basic number, *x*. This was done without consistent (reproducible) reference to species relationships and frequencies of different numbers in a clade. Likelihood models that treat polyploidy, chromosome fusion and fission as events with particular probabilities now allow reconstruction of ancestral chromosome numbers in an explicit framework. We have used a modelling approach to reconstruct chromosome number change in the large monocot family Araceae and to test earlier hypotheses about basic numbers in the family.
• *Methods* Using a maximum likelihood approach and chromosome counts for 26 % of the 3300 species of Araceae and representative numbers for each of the other 13 families of Alismatales, polyploidization events and single chromosome changes were inferred on a genus-level phylogenetic tree for 113 of the 117 genera of Araceae.
• *Key Results* The previously inferred basic numbers $x = 14$ and $x = 7$ are rejected. Instead, maximum likelihood optimization revealed an ancestral haploid chromosome number of $n = 16$, Bayesian inference of $n = 18$. Chromosome fusion (loss) is the predominant inferred event, whereas polyploidization events occurred less frequently and mainly towards the tips of the tree.
• *Conclusions* The bias towards low basic numbers (*x*) introduced by the algebraic approach to inferring chromosome number changes, prevalent among botanists, may have contributed to an unrealistic picture of ancestral chromosome numbers in many plant clades. The availability of robust quantitative methods for reconstructing ancestral chromosome numbers on molecular phylogenetic trees (with or without branch length information), with confidence statistics, makes the calculation of *x* an obsolete approach, at least when applied to large clades.

Key words: Araceae, Bayesian inference, chromosome evolution, haploid chromosome number, dysploidy, maximum likelihood inference, polyploidy.

INTRODUCTION

Chromosome numbers in angiosperms vary from $n = 2$ (Tsvelev and Zhukova, 1974; Singh and Harvey, 1975; Sokolovskaya and Probatova, 1977; Erben, 1996) over $n = 250$ (Oginuma *et al.*, 2006) and $n = 298$ (Johnson *et al.*, 1989) to $n = 320$ (Uhl, 1978). The range in animals is similar (Crosland and Crozier, 1986; Imai *et al.*, 2002). Such drastic differences in chromosome number, sometimes even within small groups, raise questions about the evolutionary direction and frequency of the implied drastic genome rearrangements. Cytogenetic studies have shown that chromosome numbers can change due to fission, fusion or genome doubling (Guerra, 2008), and there is ample evidence that such changes can contribute to speciation. It has also been inferred that a large fraction of all plant species may have polyploid genomes (Stebbins, 1971; Goldblatt, 1980; Otto and Whitton, 2000; Ramsey and Schemske, 2002; Cui *et al.*, 2006; Soltis *et al.*, 2009; Wood *et al.*, 2009; Jiao *et al.*, 2011). Chromosome counts, however, exist only for 60 000 of the 300 000–352 000 species of flowering plants (Bennett, 1998; http://www.theplantlist.org/browse/A/). Most published numbers are listed in an electronic database for

chromosome numbers, the 'Index of Plant Chromosome numbers' (http://mobot.mobot.org/W3T/Search/ipcn.html).

Given the incomplete knowledge of angiosperm chromosome numbers, evolutionary changes in chromosome numbers in most clades can only be estimated. Botanists do this by calculating a so-called basic, or monoploid, chromosome number, denoted *x*, to differentiate it from the haploid (usually the gametophytic) number *n* and the diploid (sporophytic or somatic) number *2n*. The concept of *x* goes back to Langlet (1927) who explained it using *Aconitum* as an example; if different *Aconitum* species have $n = 8$, $n = 12$, $n = 16$ and $n = $ approx. 32, their inferred monoploid number *x* is 4 (Langlet, 1927: 7). Langlet's idea took off, at least in botany, where thousands of basic chromosome numbers have been inferred, even for poorly counted groups. Thus, for flowering plants, Raven (1975, p. 760) suggested $x = 7$ as 'characteristic of all major groups of both dicots and monocots except Caryophyllidae.' Similarly, base chromosome numbers of $x = 12$ or $x = 5$ and 6 have been suggested for Poaceae (reviewed in Hilu, 2004) and $x = 7$ or $x = 12$ for Triticeae (Heslop-Harrison, 1992; Luo *et al.*, 2009). Many further examples of divergent base numbers having been calculated for a clade could be cited (Soltis *et al.*, 2005; Blöch

et al., 2009). Part of the reason why different researchers arrived at different base numbers (x) has to do with the unclear definition of x, with some treating it in Langlet's original sense as an algebraically discoverable highest common factor, others as 'the lowest *detectable* haploid number within a group of related taxa' (Stuessy, 2009: 264; italics ours), and yet others as 'the haploid number present in the initial population of a monophyletic clade' (Guerra, 2008: 340), i.e. an inferred number, since the 'initial population' will not usually have its chromosomes counted. How to make the inference is up to the investigator. Zoologists, in contrast, never became enamoured of the concept of an inferred base number x.

Criteria for inferring ancestral (perhaps no longer present) chromosome numbers from empirical counts could come from phylogenetic analyses, the relative frequencies of different haploid numbers in various species groups, cytogenetic work on closely related species or, best, a combination of all such information. Data from genomics and molecular–cytogenetic methods, such as fluorescence *in situ* hybridization (FISH)-marking chromosomes, are probably the best way to search for evidence of past chromosome number changes because they can identify synteny, fusion sites or unusual locations of centromeres, in turn providing evidence for duplications, fusions or losses (Bowers *et al.*, 2003; Lysak *et al.*, 2006; Peruzzi *et al.*, 2009). Such methods, however, may not be feasible in large clades or those with few species in cultivation.

In 2010, an approach was developed that moves the inference of chromosome number evolution to maximum likelihood (ML) character state reconstruction (Mayrose *et al.*, 2010). Mayrose *et al.* (2010) formulated probabilistic models describing the evolution of chromosome number across a phylogenetic tree. Their approach makes use of branch lengths as a proxy for time and of the frequencies of different numbers at the tips and in outgroups to infer transition rates between the different states. Ancestral chromosome numbers have previously sometimes been reconstructed using maximum parsimony (e.g. Soltis *et al.*, 2005: 178, 298–302). Parsimony, however, assigns all state transitions the same weight and disregards information contained in phylogenetic branch length, which tends to result in an underestimate of the number of transition events.

In this study we use the approach of Mayrose *et al.* (2010) to reconstruct ancestral haploid chromosome numbers in Araceae, a large and old family of monocotyledons. For a mainly tropical family, Araceae have a high number of chromosomes counts, with 862 (26 %) of their approx. 3300 species counted, including at least one species for most of the 117 genera (Petersen, 1989; Bogner and Petersen, 2007; Appendix; Supplementary Data Table S1 lists all species with their *n* and/or 2*n* counts and the respective references). Two basic chromosome numbers have been suggested for Araceae. Larsen (1969) and Marchant (1973) argued for $x = 7$, with higher numbers derived through ancient polyploidization events or ascending dysploid series. In contrast, Petersen (1993) hypothesized a base number of $x = 14$ because $2n = 28$ is especially common in the family. The former hypothesis was put forward without the benefit of a phylogenetic framework, but Petersen (and also Bogner and Petersen, 2007)

took into account morphological phylogenetic analyses (Grayum, 1990; Mayo *et al.*, 1997).

Molecular phylogenetic work over the past few years has resulted in aroid relationships at the generic level becoming relatively clear (French *et al.*, 1995; Cabrera *et al.*, 2008; Cusimano *et al.*, 2011). We here use the most recent phylogenetic analysis of Araceae to infer chromosome evolution in the family, using the model-based approach of Mayrose *et al.* (2010), in both its ML and Bayesian implementations, the latter having the advantage that uncertainty in ancestral state probabilities is readily quantified. To test the power of their method, Mayrose *et al.* (2010) first used simulated data and then four exemplar plant clades (*Aristolochia*, *Carex*, *Passiflora* and *Helianthus*) with relatively densely sampled phylogenetic trees and chromosome counts. Sampling in these clades ranged from 11 to 100 % of the species in the genera. The Araceae data set analysed here represents an entire family that is larger and older by at least an order of magnitude. This poses challenges that we tried to address by experimentally modifying character codings to take into account uncertainties in the larger genera and the 13 outgroup families.

METHODS

Family and order phylogeny

The phylogenetic tree for Araceae on which ancestral chromosome numbers were inferred in this study is based on the six-plastid marker matrix of Cusimano *et al.* (2011). Clades are named as proposed in that study. We used the ML tree from that study or an ultrametric Bayesian tree newly obtained using BEAST v. 1·6·1 (Drummond and Rambaut, 2007). In BEAST, we used the GTR + G model with four rate categories, a mean substitution rate estimated from the data, and a pure-birth Yule model as the tree prior. The GTR + G model fit the data best, as assessed with Modeltest (Posada and Crandall, 1998). The analysis was run for 37 million generations, sampling every 1000th step. The burn-in fraction, i.e. the number of trees to be discarded before runs reached stationarity, was assessed using the Tracer v. 1·4·1 program (part of the BEAST package) and AWTY (Nylander *et al.*, 2008). For one set of analyses (below), we included only Araceae. For another, we included one exemplar each of the other families of Alismatales (Stevens, 2001 onwards), using branch lengths of 0·01 except for Tofieldiaceae (*Tofieldia*), which was the outgroup used by Cusimano *et al.* (2011) and had an empirical branch length.

Chromosome number coding

Total numbers of genera and species of Araceae were taken from the website Creating a Taxonomic eScience (CATE; http://www.cate-araceae.org/) and then updated by the Araceae specialist Josef Bogner (see Acknowledgements). Of the 117 currently recognized genera of Araceae, 29 are monospecific (and hence can be coded unambiguously for chromosome number), 19 have just two species, 31 have 3–10 species, 25 have 11–50 species and 13 have >50 species. Araceae chromosome counts were compiled from original literature

(Supplementary Data Table S1, available online), checking the generic assignment of each species against the current classification and for synonymy. Chromosome numbers for four monotypic genera were contributed by J. Bogner and E. Vosyka (see Acknowledgements) and are newly reported here: *Filarum manserichense* Nicolson (M. Sizemore *s.n.*, voucher in the herbarium M), *Hestia longifolia* (Ridl.) S. Y. Wong & P. C. Boyce (J. Bogner 3003, M), *Philonotion americanum* (A. M. E. Jonker & Jonker) S. Y. Wong & P. C. Boyce (J. Bogner 2911, M) and *Pichinia disticha* S. Y. Wong & P. C. Boyce (P. C. Boyce *s.n.*, M; Supplementary Data Table S1). One genus was coded as unknown (X), namely the monotypic *Schottariella*, the chromosomes of which have not been counted. The presence of B chromosomes was not coded. Overall, our phylogenetic analysis includes 113 of the 117 accepted genera of Araceae, with 112 of them coded for haploid chromosome number (Appendix).

Chromosome numbers were coded in three ways to address the problem of genera with more than one chromosome number. First, we coded all reported numbers for each genus, regardless of frequency in different species, but excluding odd numbers (Appendix, column 5; Supplementary Data Table S1). This resulted in 55 genera coded as polymorphic. Our second coding scheme ('reduced polymorphism' coding) took into account the frequency of different numbers and treated the most common as the ancestral state (Appendix, column 7; Supplementary Data Table S1). For example, Lemnoideae have many different chromosome numbers, but $n = 20$ is especially common (Landolt, 1986; Appendix, Supplementary Data Table S1). For genera with numbers suggesting different ploidy levels, we used the lowest haploid chromosome number (e.g. *Arum*). Polymorphisms could thus be reduced to two states (chromosome numbers) per genus or even a single haploid number, leaving 34 instead of 55 genera with polymorphic numbers. In a third coding scheme ('informed' coding), we took into account molecular phylogenetic analyses for the genera *Philodendron* (Gauthier *et al.*, 2008), *Biarum* and *Typhonium* (Cusimano *et al.*, 2010), and assigned the state (chromosome number) found in the early-branching species to the entire genus. The numbers thus inferred were compared with those inferred by Bogner and Petersen (2007). This third approach left just ten genera coded as polymorphic with maximally two states (Appendix, column 8; Supplementary Data Table S1, Supplementary Data Figs S1 and S2). In this third scheme, *Lazarum*, a genus of 23 species with a few chromosome counts and insufficient phylogenetic information (Matthew Barrett, Botanic Gardens & Parks Authority, West Perth; personal communication, 2011) was coded as 'unknown' (X) because no ancestral haploid number could be inferred. In all cases, changes among character states (i.e. chromosome numbers) were assigned equal probability.

The remaining families of Alismatales were coded as follows: Alismataceae $n = 7, 8$; Aponogetonaceae $n = 12, 16, 19$; Butomaceae $n = 7, 8, 10, 11, 12$; Cymodoceaceae $n = 7, 8, 10, 14, 15$; Hydrocharitaceae $n =$ notably variable; Juncaginaceae $n = 6, 8, 15$; Maundiaceae only *Maundia triglochinoides*, no chromosome count reported; Posidoniaceae $n = 10$; Ruppiaceae $n = 8–12, 15$; Potamogetonaceae $n = 7, 12, 14–18$; Scheuchzeriaceae $n = 11$; Tofieldiaceae $n = 15$; Zosteraceae $n = 6, 9, 10$ (numbers from Stevens, 2001 onwards). Those of these families with more than one number listed by Stevens were coded as polymorphic in all analyses. The above-described three coding schemes were first run on the phylogenetic tree that included only Araceae and then on the tree that included the 13 outgroups, resulting in six analyses (labelled A1–A6 in Table 1).

Inference of chromosome number change

For ML and Bayesian phylogenetic inferences of ancestral haploid chromosome numbers, we relied on the chromEvol program v. 1·2 of Mayrose *et al.* (2010; http://www.zoology.ubc.ca/prog/ chromEvol.html). This implements eight models of chromosome number change (Table 2), two more than described in the original paper. The models include the following six parameters: polyploidization (chromosome number duplication with rate ρ, 'demi-duplication' or triploidization with rate μ) and dysploidization (ascending, chromosome gain rate λ; descending, chromosome loss rate δ) and two linear rate parameters, λ_1 and δ_1, for the dysploidization rates λ and δ, allowing them to depend on the current number of chromosomes. Four of the models have a constant rate, whereas the other four include the two linear rate parameters. Both model sets also have a null model that assumes no polyploidization events. We fitted all models to the data, each with 10 000 simulations to compute the expected number of changes of the four transition types along each branch. The maximum number of chromosomes was set to $10\times$ higher then the highest number found in the empirical data, and the minimum number was set to 1. The null hypothesis (no polyploidy) was tested with likelihood ratio tests using the Akaike information criterion (AIC).

We also ran an analysis, using the informed polymorphism-coding scheme, but excluding *Calla* because of its unclear relationships in Araceae (Cusimano *et al.*, 2011). For a final sensitivity test, we again used the informed coding scheme but the non-ultrametric ML phylogenetic tree from Cusimano *et al.* (2011) instead of the ultrametric tree used in the remaining analyses.

RESULTS

The results obtained in the six analyses (A1–A6) are summarized in Table 1. The three-parameter constant-rate model (Mc2), with the chromosome duplication rate equal to the demi-duplication rate, was the best explanation of the empirical data in all analyses. All analyses rejected the null model of no polyploidy with high significance ($P < 0.999$). The inferred rates of change, chromosome numbers at nodes (and their probability) and numbers of events were similar regardless of which of the three schemes for polymorphism coding was applied. We therefore show the results obtained from Bayesian and ML analyses with the most conservative coding scheme, namely the one including all polymorphisms and all outgroups (Table 1, A1; Figs 1 and 2). For comparison, the results from analysis A6, without outgroups and the phylogenetically informed coding (Appendix, column 8), can be found in Supplementary Data Figs S1 and S2.

TABLE 1. *Results from the six analyses (A1–A6) carried out to infer chromosome number changes in Araceae under Bayesian and maximum likelihood optimization*

Analysis	Tree: outgroups	Coding scheme All poly.	Coding scheme Red. poly.	Coding scheme Inf.	Best model	LogLik	AIC	Rate parameters δ	Rate parameters λ	Rate parameters ρ	Rate parameters μ	Events inferred with PP >0.5 Losses	Gains	Dupl.	Demi.	Chromosome no. at Araceae root node Bayes; Best n; PP	Chromosome no. at Araceae root node Bayes; 2nd best n; PP	ML	Chromosome no. ranges at Araceae root node n	Sum PP	Chromosome no. ranges at Araceae root node n	Sum PP
A1	+	+			Mc2	−219·5	445	45·9	3·9	6·9	–	98·1	8·4	14·3	14·3	18; 0·18	16; 0·16	16	16–18	0·5	8–18	0·9
A2	+		+		Mc2	−236·4	478·9	56·4	0	6·3	–	112·2	0	11·5	13	18; 0·26	17; 0·13	16	17–19	0·51	10–20	0·85
A3	+			+	Mc2	−245·7	497·3	58·2	0	5·7	–	120·1	0	11·9	13·9	18; 0·26	19; 0·12	17	17–19	0·52	10–20	0·9
A4	–	+			Mc2	−196·6	399·1	50·4	1·8	6·6	–	86·6	3·2	10·5	9·3	18; 0·38	17; 0·3	17	17–19	0·86		
A5	–		+		Mc2	−213·2	432·4	53·6	0	5·6	–	87·2	0	9·8	9·4	18; 0·42	17; 0·23	17	17–19	0·9		
A6	–			+	Mc2	−222·4	450·7	58·1	0	5·4	–	94·4	0	9·7	10·5	18; 0·37	19; 0·34	18	17–19	0·85		

Only the best-fitting models are shown. Tree (column 2) refers to whether outgroups were included or not; coding scheme refers to how genera with polymorphic haploid chromosome numbers were coded. All poly., all chromosome number polymorphism coded (scheme 1); Red. poly., reduced polymorphism coding (scheme 2); Inf., phylogenetically informed coding (scheme 3). Best model, Mc2 (constant rate model with duplication rate ρ and demi-duplication rate μ; compare Table 2); Logarithmic likelihood (LogLik) and AIC scores; rate parameters (δ = chromosome loss rate, λ = chromosome gain rate, ρ = duplication rate, μ = demi-duplication rate); frequency of the four possible event types with a posterior probability (PP) > 0·5; haploid chromosome number inferred at the root node under Bayesian optimization with the respective PP, and under maximum likelihood (ML). The last column shows the chromosome number range inferred for the root node, each with its PP.

The loss rate δ ranges from 45·9 (Table 1, A1) to 58·2 (A3), and the polyploidization rate $\rho = \mu$ from 5·4 (A6) to 6·9 (A1). A gain rate λ is inferred only for models A1 (3·9) and A4 (1·8, analyses with all polymorphisms coded). The number of events inferred with a probability of >0·5 is higher in the analyses using the tree with outgroups than in that without outgroups, simply because it has more branches. Inferred chromosome loss events range from 98·1 (A1) to 120·1 (A3), duplications from 11·5 (A2) to 14·3 (A1) and demi-duplications from 13 (A2) to 14·3 (A3)); in A1, 8·4 chromosome gain events were inferred, whereas, in the tree without outgroups, the number of losses ranges from 86·6 (A4) to 94·4 (A6), that of duplications from 9·7 (A6) to 10·5 (A4) and that of demi-duplications from 9·3 (A4) to 10·5 (A6); finally in A4, 3·2 chromosome gain events were inferred (Table 1, Fig. 1 and Supplementary Data Fig. S1, Bayesian inference). In the Bayesian analyses, the haploid chromosome number at the root with the highest posterior probability (PP) was $n = 18$, and support for this number was higher in analyses without outgroups (0·37–0·42) than in those with outgroups (0·18–0·26, Table 1). Similarly, a range of $n = 17$–19 at the root node had a PP of $\geq 0·85$ without outgroups, but only $\leq 0·52$ when outgroups were included (Table 1). A broader range of ancestral numbers [$n = 8$–18 (A1); $n = 10$–20 (A2, A3)] could be inferred with higher PP (>0·85, Table 1, Fig. 1 and Supplementary Data Fig. S1). In the ML analyses with outgroups (Fig. 2), the most likely haploid number at the root was $n = 16/17$, and without outgroups it was 17/18 (Table 1; Supplementary Data Fig. S2).

To describe inferred chromosome evolution in Araceae, we focus on the Bayesian inference of the most conservative analysis scheme A1 depicted in Fig. 1. Starting from the root node, chromosome numbers decreased, becoming $n = 15$ along the branch leading to the *Spirodela* clade (PP = 0·32; $n = 16$: PP = 0·29), $n = 15$ in Araceae (PP = 0·55; $n = 14$: PP = 0·21), and $n = 14$ in the *Podolasia* clade (PP = 0. 62; $n = 15$: PP = 0·24). The number $n = 14$ is inferred with increasing probability as one moves up the phylogenetic tree towards the present. It has 0·77 PP in Aroideae and 0·99 PP in the *Ambrosina* clade.

Increases in chromosome number are inferred as deriving from (demi-) duplication events, never via single chromosome gains (centric fission), whereas decreases in chromosome number are inferred as resulting from chromosome loss (fusion). The most likely events (PP >0·5) predicted by the best-fitting model are descending dysploidy (98·1 events), and these are inferred both on branches leading to major clades (e.g. Pothoideae, Lasioideae and Spathicarpeae) and on terminal branches. The only chromosome gain event in Araceae inferred with high probability occurred on the branch leading to *Scaphispatha* ($n = 14$). Polyploidization events (29 in total, Fig. 1) occur mainly towards the tips of the tree (*Gymnostachys*, *Alloschemone*, *Urospatha*, *Anubias*, *Montrichardia*, Cryptocoryneae, *Calla*, *Filarum* and *Peltandra*). Only three polyploidization events are inferred deeper in the tree: a genome duplication on the branch leading to the *Rhaphidophora* (Fig. 1) clade (from $n = 15$ to $n = 30$), a demi-duplication on the branch leading to the *Zantedeschia* clade (from $n = 14$ to $n = 21$) and one
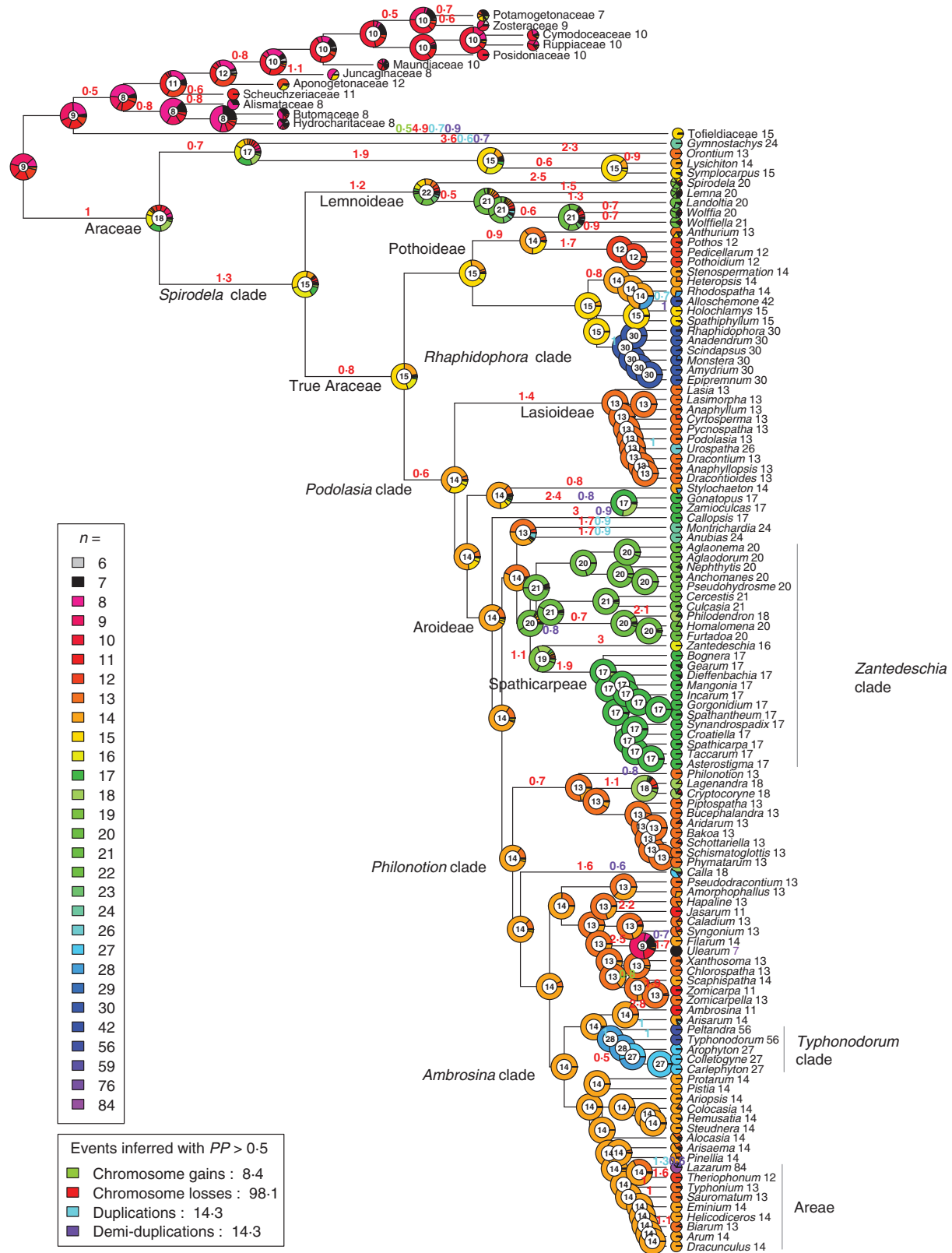
Fig. 1. Chromosome number evolution in Araceae inferred under Bayesian optimization, with outgroups included and all polymorphic chromosome states coded (analysis A1 in Table 1). Pie charts at nodes and tips represent the probabilities of the inferred chromosome number(s); numbers inside charts have the highest probability. Numbers at the tips are chromosome numbers inferred with the highest probability, i.e. the inferred ancestral haploid chromosome number for each genus. Numbers above branches represent the inferred frequency of those of the four possible events (gains, losses, duplications and demi-duplications) that had a probability >0·5. The colour coding of chromosome numbers and event types is explained in the insets.
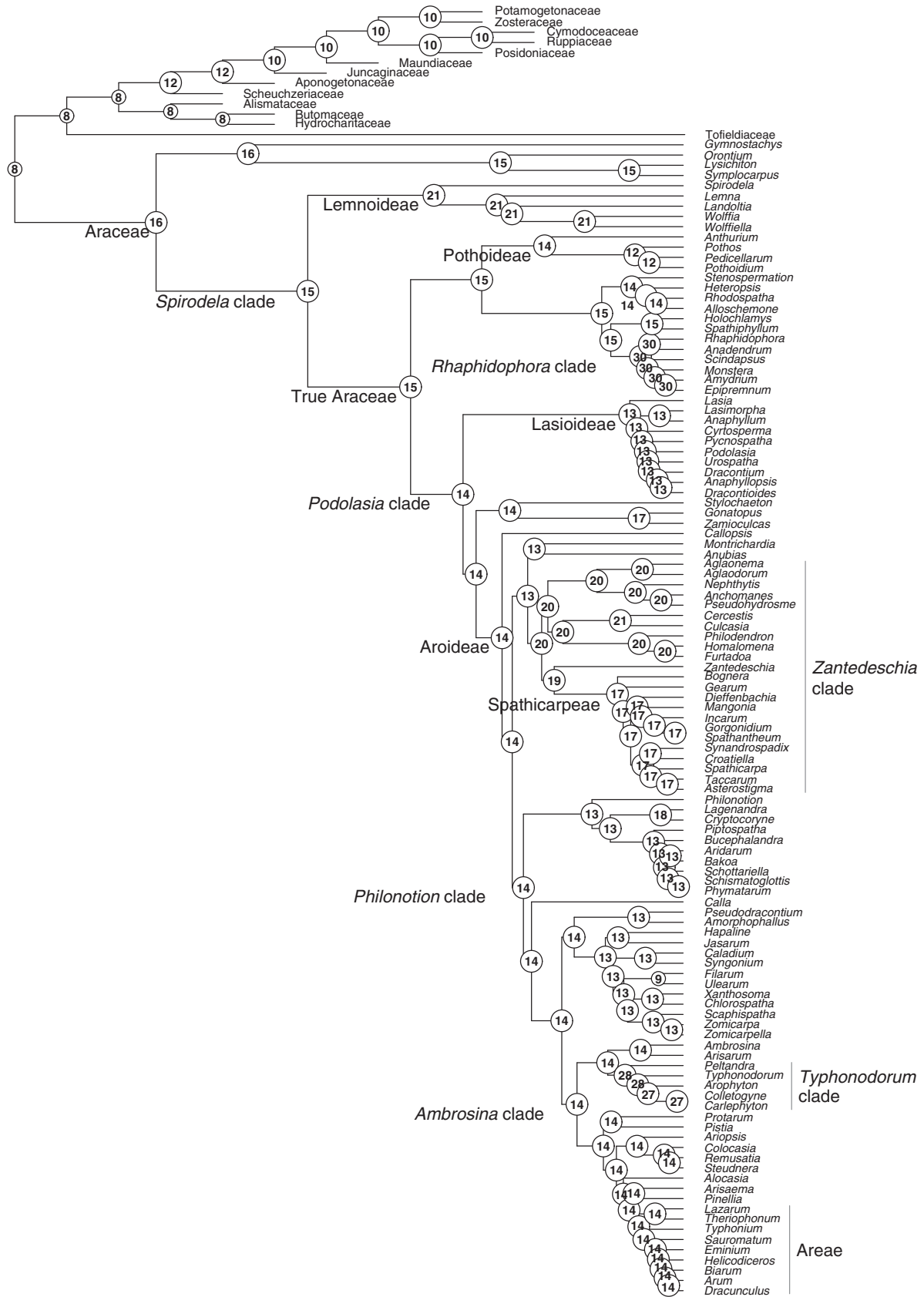
FIG. 2. Chromosome number evolution in Araceae inferred under maximum likelihood optimization, with outgroups included and all polymorphic chromosome states coded (analysis A1 in Table 1).

TABLE 2. *The eight models of chromosome number evolution implemented in the software of* Mayrose et al. *(2010), indicating the considered parameter estimates (δ, λ, ρ, μ, δ₁, λ₁), the number of parameters included, and, in the case of μ, with which condition*

Model	δ	λ	ρ	μ	δ_1	λ_1	No. of parameters
Mc1	+	+	+	−	−	−	3
Mc2	+	+	+	$\rho = \mu$	−	−	3
Mc3	+	+	+	$\rho \neq \mu$	−	−	4
Mc0	+	+	$\rho = 0$	$\mu = 0$	−	−	2
Ml1	+	+	+	−	+	+	5
Ml2	+	+	+	$\rho = \mu$	+	+	5
Ml3	+	+	+	$\rho \neq \mu$	+	+	6
Ml0	+	+	$\rho = 0$	$\mu = 0$	+	+	4

Mc indicates models with constant rates, and Ml models that include linear rate parameters (δ_1, λ_1). Zero indicates the respective null model.

duplication event on the branch leading to the *Typhondorum* clade (from $n = 14$ to $n = 28$).

Results of the two additional analyses (inclusion/exclusion of *Calla*; ultrametric or non-ultrametric trees) did not yield results substantially different from those obtained in analysis A6 and shown in Supplementary Data Fig. S1. Model Mc2 remained the best-fitting model, and chromosome number reconstructions at nodes and change rates were similar.

DISCUSSION

The results presented here provide an example of the power of ML-based or Bayesian inference of chromosome number changes. The new approach, which distinguishes (and separately infers) chromosome gains, losses, polyploidization and demi-ploidization, not only reconstructs numbers at particular phylogenetic nodes, but also infers rates of change throughout the phylogenetic tree. Equally importantly, Bayesian *PP*s yield a statistically well-understood measure of confidence in the results. Most previous ancestral chromosome numbers, in contrast, have been inferred without confidence assessment (examples and critical discussion in Soltis *et al.*, 2005). The experiments we carried out with the different coding schemes for genera polymorphic for chromosome number revealed surprising robustness of the states inferred at interior nodes, although as expected the inclusion or exclusion of outgroups (in our case 13 families) affected the number inferred for the basal-most node, albeit only slightly (Table 1). The results of the present study further confirm that model-based chromosome inference works well even with large data matrices; the largest of the four matrices analysed by Mayrose *et al.* (2010) had 107 terminals, and the present tree had 126.

Chromosome fusion (loss) appears to be the predominant pattern in the evolution of chromosome number in Araceae; polyploidization events are much less frequent and apparently occurred mainly towards the tips of the tree. However, ancient polyploidization events may be harder to detect than recent ones, because of the genomic restructuring that follows polyploidization. Only detailed studies, perhaps involving chromosome painting techniques, will reveal how rapid intergenomic rearrangements have occurred after genome doubling, perhaps especially following hybridization (Hayasaki *et al.*, 2000; Lim *et al.*, 2008; Peruzzi *et al.*, 2009; Tu *et al.*, 2009).

In general, basic chromosome numbers inferred according to Langlet's (1927) approach, as the lowest detectable or somehow calculated haploid number within a group of related taxa, will be low, simply because of the way they are arrived at (see Introduction for Langlet's original example). For Araceae, the hypothesized ancestral numbers were $x = 14$ or $x = 7$ (Larsen, 1969; Marchant, 1973; Petersen, 1993). The present study instead inferred an ancestral haploid number of $n = 16$ (under ML) or $n = 18$ (with Bayesian inference) and, moreover, an evolutionary trend from higher to lower numbers, rather than the other way around. One needs to keep in mind that none of the earlier studies (Larsen, 1969; Marchant, 1973; Petersen, 1993) included Lemnoideae in Araceae, a taxonomic difference that greatly affects the range of chromosome numbers found in early-diverging clades (Figs 1 and 2). It is also likely that the high frequency of $2n = 28$ in the well-counted unisexual Aroideae unduly influenced the hypotheses about x being 7 or 14. Finally, the earlier hypotheses were developed without the relatively complete and solid phylogenetic information that is available today.

Nevertheless, any inferences about character evolution from a taxon sampling of just 112 representatives, however well coded their states may be, must be regarded with caution. Every genus with more than one species must have its own, perhaps complex, history of cytogenetic change. It is also conceivable that dysploidy rates might change in different parts of the tree (e.g. in clades of taxa living in different environments) and that relatively derived and rapidly radiating clades, perhaps with frequent hybridization, might have different rates of polyploidization than older, genetically isolated groups. The phylogenetically informed coding scheme (our scheme three) may be the best way of coding ancestral haploid chromosome numbers in larger clades (here genera), an idea that could be tested by cytological work in small genera with solid phylogenetic hypotheses, such as *Arum* (e.g. Espíndola *et al.*, 2010).

Given the inferred high ancestral haploid numbers, chromosome fusions (neutrally termed 'losses' in the models of Mayrose *et al.*, 2010) must have been common during evolution of Araceae. This hypothesis now needs to be tested. Large chromosomes in Araceae, with distally positioned centromeres, may be the result of fusion between smaller metacentric chromosomes (Petersen, 1993). If so, one expects to find interstitial telomeric sites. With probes, using primer pairs homologous to the basic plant telomeric repeats, one can visualize these regions (Ijdo *et al.*, 1991; Weiss-Schneeweiss *et al.*, 2004). Such chromosome preparations are now being carried out in our laboratory on *Typhonium* species with suspected chromosome fusion (predicted from high or low chromosome numbers in species of known phylogenetic relationships).

The results of the present study suggest that quantitative methods for inferring ancestral haploid numbers should replace inferences that rely on algebraically finding the greatest common factor for a series of numbers or on interpreting the lowest available haploid count as the ancestral condition.

The new approaches also yield a measure of statistical confidence or estimates of the rates of polyploidization, fusion or fission, We suggest that the concept 'x', which sets botanists apart from zoologists, be retained only in the context of small species groups in which the history of polyploidy is known in detail (Vanzela *et al.* 2003).

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxford-journals.org and consist of the following. Table S1: chromosome counts for species of Araceae with references. Figure S1: chromosome number evolution in Araceae inferred under Bayesian optimization, with phylogenetically informed coding and outgroups excluded. Figure S2: chromosome number evolution in Araceae inferred under maximum likelihood optimization, with phylogenetically informed coding and outgroups excluded.

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APPENDIX

The 117 genera of Araceae with number of species, number and percentage of species with chromosome counts, diploid chromosome numbers and coded ancestral haploid chromosome numbers in the three coding schemes used in this study (see Methods). X = unknown.

	Genera	Spp. number	Spp. counted	%	Counted diploid chromosome numbers 2n =	All polymorphic n =	Reduced polymorphic n =	Informed n =
1	*Aglaodorum*	1	1	100	40	20	20	20
2	*Aglaonema*	23	6	26	14, 40, 100	7, 20, 50	7, 20, 50	20
3	*Alloschemone*	2	1	50	84	42	42	42
4	*Alocasia*	107	17	16	24, 26. 28, 40,42, 56, 68, 70, 84	12, 13, 14, 20, 21, 28, 34, 35, 42	12, 13, 14, 20, 21, 28, 34, 35, 42	14
5	*Ambrosina*	1	1	100	22	11	11	11
6	*Amorphophallus*	196	47	24	26, 28, 39	13, 14	13, 14	13
7	*Amydrium*	5	2	40	60	30	30	30
8	*Anadendrum*	11	3	27	60	30	30	30
9	*Anaphyllopsis*	3	1	33	26	13	13	13
10	*Anaphyllum*	2	2	100	26	13	13	13
11	*Anchomanes*	6	3	50	40	20	20	20
12	*Anthurium*	903	171	19	14, 20, 24, 26, 28, 29, 30 + Bs, 34, 36, 40, 48, 49, 56, 60, 84, approx. 90, approx. 124	7, 13, 15, 17, 18, 30	7, 13, 15, 17, 18, 30	15
13	*Anubias*	8	8	100	48	24	24	24
14	*Apoballis*	12	6	50	26, 39, 56	13, 28	13	13
15	*Aridarum*	10	4	40	24, 26	12, 13	12, 13	12, 13
16	*Ariopsis*	2	1	50	28, 84, 86	14, 42, 43	14	14
17	*Arisaema*	150	97	65	20, 24, 26, 28, 32,42, 48, 52, 56, 64, 70, 72, 84, 112, 140, 168	10, 12, 13, 14, 16, 21, 24, 26, 28, 32, 42, 56, 70, 84	10, 12, 13, 14, 16, 21, 24, 26, 28, 32, 42, 56, 70, 84	14
18	*Arisarum*	4	2	50	14, 28, 42, 52, 56	7, 14, 21, 26, 28	7, 14, 21, 26, 28	14
19	*Arophyton*	7	6	86	38, 40, 54, approx. 76	19, 20, 27	19, 20, 27	19
20	*Arum*	29	26	90	28, 29, 30, 42, 56, 63, 70, 84	14, 15, 21, 28, 35, 42	14	14
21	*Asterostigma*	8	2	25	34	17	17	17
22	*Bakoa*	2	2	100	26	13	13	13
23	*Biarum*	21	12	57	16, 18, 22, 24, 26, 32, 36, 40, 74, approx. 96, 98, 108	8, 9, 11, 12, 13, 16, 18, 20, 37, 49, 54	8, 9, 11, 12, 13, 16, 18, 20, 37, 49, 54	13
24	*Bognera*	1	1	100	34	17	17	17
25	*Bucephalandra*	3	3	100	26	13	13	13
26	*Caladium*	12	6	50	19, 22, 26, 28, 30	11, 13, 14, 15	11, 13, 14, 15	13, 14
27	*Calla*	1	1	100	36, 54, 60, 72	18, 27, 30, 36	18	18
28	*Callopsis*	1	1	100	36	17	17	17
29	*Carlephyton*	3	3	100	54, 108	27, 54	27	27
30	*Cercestis*	10	6	60	approx. 36, 42	21	21	21
31	*Chlorospatha*	28	2	7	26	13	13	13
32	*Colletogyne*	1	1	100	44, 46, 54	22, 23, 27	27	27
33	*Colocasia*	16	5	31	26, 28, 30, 36, 38, 42, 44, 46, 48, 52, 58, 84, 116	13, 14, 15, 18, 19, 21, 22, 23, 24, 26, 42, 58	13, 14, 15, 18, 19, 21, 22, 23, 24, 26, 42, 58	14
34	*Croatiella*	1	1	100	34	17	17	17
35	*Cryptocoryne*	60	64	107	20, 22, 28, 30, 33, 34, 36, 42, 54, 56, 66, 68, 70, 72, 85, 88, 90, 102, 112, approx. 132	10, 11, 14, 15, 17, 18, 21, 27, 28, 33, 34, 35, 36, 44, 45, 51, 56	10, 11, 14, 15, 17, 18, 21, 27, 28, 33, 34, 35, 36, 44, 45, 51, 56	17, 18
36	*Culcasia*	24	9	38	approx. 40, 42	21	21	21
37	*Cyrtosperma*	12	4	33	24, 26	12, 13	12, 13	13
38	*Dieffenbachia*	57	14	25	34, 36, 40, 44, 68	17, 18, 20, 22, 34	17	17
39	*Dracontioides*	2	1	50	26	13	13	13
40	*Dracontium*	24	5	21	26	13	13	13
41	*Dracunculus*	2	2	100	28, 32	14, 16	14	14
42	*Eminium*	9	3	33	28	14	14	14
43	*Epipremnum*	15	3	20	60, 70, 84	30, 35, 42	30, 35, 42	30
44	*Filarum*	1	1	100	28	14	14	14
45	*Furtadoa*	2	1	50	40	20	20	20
46	*Gearum*	1	1	100	34, 68	17, 34	17	17
47	*Gonatopus*	5	4	80	34, approx. 68	17	17	17
48	*Gorgonidium*	8	3	38	34	17	17	17
49	*Gymnostachys*	1	1	100	48	24	24	24
50	*Hapaline*	8	2	25	26, 28	13, 14	13, 14	13, 14

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TABLE *Continued*

	Genera	Spp. number	Spp. counted	%	Counted diploid chromosome numbers $2n =$	All polymorphic $n =$	Reduced polymorphic $n =$	Informed $n =$
51	*Helicodiceros*	1	1	100	56	14	14	14
52	*Hestia*	1	1	100	26	13	13	13
53	*Heteropsis*	17	1	6	26–28	13, 14	13, 14	14
54	*Holochlamys*	1	1	100	30, 60	15	15	15
55	*Homalomena*	117	24	21	38, 40, 42, 56	19, 20, 21, 28	19, 20, 21, 28	20
56	*Incarum*	1	1	100	34	17	17	17
57	*Jasarum*	1	1	100	22	11	11	11
58	*Lagenandra*	15	14	93	32, 36, approx. 72	16, 18	16, 18	18
59	*Landoltia*	1	1	100	40,46, 50	20, 23, 25	20	20
60	*Lasia*	2	1	50	26	13	13	13
61	*Lasimorpha*	1	1	100	26	13	13	13
62	*Lazarum*	23	2	9	approx. 118, 130, 152, approx. 160,168	59, 65, 76, 84	59, 65, 76, 84	X
63	*Lemna*	13	11	85	20, 30, 36, 40, 42, 44, 50, 60, 63, 64, 70, 80, 84, 126	10, 15, 18, 20, 21, 22, 25, 30, 32, 35, 40, 42, 63	20	20
64	*Lysichiton*	2	2	100	28	14	14	14
65	*Mangonia*	2	1	50	34	17	17	17
66	*Monstera*	39	5	13	24, 56, 58, 60	12, 28, 29, 30	30	30
67	*Montrichardia*	2	1	50	48	24	24	24
68	*Nephthytis*	6	5	83	36, 40, 60	18, 20, 30	18, 20	18, 20
69	*Ooia*	2	1	50	26	13	13	13
70	*Orontium*	1	1	100	26	13	13	13
71	*Pedicellarum*	1	1	100	24	12	12	12
72	*Peltandra*	2	1	50	112	56	56	56
73	*Philodendron*	483	31	6	26, 30, 32, 34, 36, 48, 54	13, 15, 16, 17, 18, 24, 27	13, 15, 16, 17, 18, 24, 27	17, 18
74	*Philonotion*	3	1	33	26	13	13	13
75	*Phymatarum*	1	1	100	26, 28	13	13	13
76	*Pichinia*	1	1	100	26	13, 14	13, 14	13
77	*Pinellia*	9	9	100	20, 26, 28, 39, 42, 52, 54, 72, 78, 90, 91, 99, 104, 108, 115, 116, 117, 128, 129	10, 13, 14, 21, 26, 27, 36, 39, 45, 52, 54, 58, 64	10, 13, 14, 21, 26, 27, 36, 39, 45, 52, 54, 58, 64	13
78	*Piptospatha*	10	6	60	26, 39	13	13	13
79	*Pistia*	1	1	100	14, 28	7, 14	7, 14	14
80	*Podolasia*	1	1	100	26	13	13	13
81	*Pothoidium*	1	1	100	24	12	12	12
82	*Pothos*	57	3	5	24, 36, 60	12, 18, 30	12	12
83	*Protarum*	1	1	100	28	14	14	14
84	*Pseudodracontium*	7	2	29	26	13	13	13
85	*Pseudohydrosme*	2	1	50	approx. 40	20	20	20
86	*Pycnospatha*	2	2	100	26	13	13	13
87	*Remusatia*	4	4	100	20, 28, 30, 42, 56	10, 14, 15, 21, 28	10, 14, 15, 21, 28	14
88	*Rhaphidophora*	98	8	8	26, 42, 54, 56, 60, approx. 120	13, 21, 27, 28, 30	28, 30	28, 30
89	*Rhodospatha*	29	3	10	28, 56, 60	14, 28, 30	14, 28	14
90	*Sauromatum*	9	7	78	26, 52, 54, 104	13, 26, 27, 52	13	13
91	*Scaphispatha*	2	1	50	28	14	14	14
92	*Schismatoglottis*	100	15	15	26, 30, 39, 52	13, 15, 26	13	13
93	*Schottariella*	1	0	0	–	X	X	X
94	*Scindapsus*	35	8	23	48, 60 (42, 56, 58, 64, 70, 112), approx. 110	28, 30	28, 30	28, 30
95	*Spathantheum*	2	2	100	34	17	17	17
96	*Spathicarpa*	4	1	25	34	17	17	17
97	*Spathiphyllum*	49	9	18	30, 60	15, 30	15	15
98	*Spirodela*	3	2	67	20, 30, 32, 36, 38, 40, 50, 80	10, 15, 16, 18, 19, 20, 25, 40	15, 20	15, 20
99	*Stenospermation*	50	4	8	28	14	14	14
100	*Steudnera*	9	4	44	28, 36,56	14, 18, 28	14	14
101	*Stylochaeton*	18	4	22	28, 56	14, 28	14, 28	14
102	*Symplocarpus*	5	2	40	30, 60	15, 30	15, 30	15
103	*Synandrospadix*	1	1	100	34	17	17	17
104	*Syngonium*	35	9	26	22, 24, 26, 28	11, 12, 13, 14	14	14
105	*Taccarum*	6	1	17	34	17	17	17
106	*Theriophonum*	5	5	100	16, 24, 32 (14, 18)	8, 12, 16	8	8
107	*Typhonium*	68	8	12	10, 16, 18, 20, 26, 36, 52,65	5, 8, 9, 10, 13, 18, 26	5, 6, 7, 8, 9, 10, 13, 18, 26	8, 13

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	Genera	Spp. number	Spp. counted	%	Counted diploid chromosome numbers 2n =	All polymorphic n =	Reduced polymorphic n =	Informed n =
108	*Typhonodorum*	1	1	100	112	56	56	56
109	*Ulearum*	2	2	100	14	7	7	7
110	*Urospatha*	12	1	8	52	26	26	26
111	*Wolffia*	11	8	73	16, 20, 22, 23, 30, 40, 42, 46, 50, 60, 62, 63, 70, 80	8, 10, 11, 15, 20, 21, 23, 25, 30, 31, 35, 40	20	20
112	*Wolffiella*	10	7	70	20, 40, 42, 50, 70	10, 20, 21, 25, 35	20	20
113	*Xanthosoma*	75	11	15	22, 26, 39, 52	11, 13, 26	11, 13, 26	13
114	*Zamioculcas*	1	1	100	34	17	17	17
115	*Zantedeschia*	8	7	88	32	16	16	16
116	*Zomicarpa*	3	2	67	20, 22	10, 11	10, 11	10
117	*Zomicarpella*	2	1	50	26	13	13	13
	Total	3309	847					
	Mean			61				