

Molecular phylogenetics and new (infra)generic classification to alleviate polyphyly in tribe Hydrangeeae (Cornales: Hydrangeaceae)

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Abstract Tribe Hydrangeeae of Hydrangeaceae currently contains nine morphologically diverse genera, many of which are well-known garden ornamentals. Previous studies have shown eight of these genera to be phylogenetically nested within *Hydrangea*, rendering the latter polyphyletic. To clarify the phylogeny of tribe Hydrangeeae, the present study sequenced four chloroplast regions and ITS for an extensive set of taxa, including the type for all nine genera involved. The resulting phylogenetic hypotheses corroborate the polyphyly of *Hydrangea*. Since polyphyletic taxa are deemed unacceptable by both sides in the ongoing debate concerning the adherence to strict monophyly in biological classifications, a new (infra)generic classification for tribe Hydrangeeae is proposed. In order to create a stable, evolutionary informative classification a broader circumscription of the genus *Hydrangea* is proposed, to include all eight satellite genera of the tribe. Such treatment is considered highly preferable to an alternative where *Hydrangea* is to be split into several morphologically potentially unidentifiable genera. To facilitate the acceptance of the new classification proposed here, and in order to create a classification with high information content, the familiar generic names were maintained as section names where possible.

Keywords classification; Cornales; *Hydrangea*; molecular phylogeny; taxonomy

Supplementary Material Electronic Supplement (Tables S1–S2; Figs. S1–S7) and sequence alignments are available in the Supplementary Data section of the online version of this article at <http://www.ingentaconnect.com/content/iapt/tax>

■ INTRODUCTION

Over the past few decades, rapid advances in DNA technologies have brought about an increase in the use of phylogenetic hypotheses in taxonomy (e.g., phylogenetic systematics; Hennig, 1966). Indeed, the majority of contemporary taxonomic studies attempt to establish natural, genealogy-based classifications, guided by phylogenetic hypotheses. Therefore, a consensus seems to have arisen that common descent should play a major role in biological classification (Xiang X.G. & al., 2012). Disagreements, however, still exist with respect to the treatment of paraphyletic taxa, with two sides locked in ongoing debate (reviewed in: Hörandl & Stuessy, 2010; Schmidt-Lebuhn, 2012). On the one hand, the school of evolutionary systematics advocates a classification system with a high information content (Stuessy, 1987; Van Wyk, 2007; Hörandl, 2010; Mayr & Bock, 2002) and practicability (Brummit, 2002; Brickel & al., 2008), reflecting natural processes. In this philosophy, shared descent is viewed as an important character for grouping taxa, but an emphasis is placed on degrees of

divergence and similarity between elements of a certain taxon (Hörandl & Stuessy, 2010). As a consequence, evolutionary systematists advocate the recognition of paraphyletic taxa, as these are argued to reflect similarity, high information content and practicability. The school of phylogenetic (or cladistic) systematics, on the other hand, proposes strict adherence to monophyletic (holophyletic) taxa, recognized by the presence of synapomorphic characters. This school argues that monophyletic groups are objective entities, considering all taxa above species level as human-devised, artificial constructs. Therefore, since paraphyletic taxa are based on a subjective idea of what is “divergent enough” (Schmidt-Lebuhn, 2012), these entities are rejected as artificial classes created to emphasize particular characters or divergence (Donoghue & Cantino, 1988; Ebach & al., 2006). Here, some of the prominent discussion points between both schools are illustrated with the taxonomy of Hydrangeaceae tribe Hydrangeeae. This group provides an interesting case study for solving complex classification problems due to the presence of (1) paraphyletic groups both at genus level and below, (2) a large polyphyletic

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assemblage, and (3) important horticultural representatives with very distinct morphology.

The asterid family Hydrangeaceae (Cornales) is an assemblage of 17 currently recognized genera, containing ca. 270 accepted species. In the most recent revision of the classification of Hydrangeaceae, Hufford & al. (2001) combined results from previous morphological (Hufford, 1997) and molecular (Soltis & al., 1995) studies to support the split of Hydrangeaceae into subfamilies Jamesioideae and Hydrangeoideae. The 15 genera contained in subfamily Hydrangeoideae were classified in tribes Philadelphae and Hydrangeae. The focal group of the present study, tribe Hydrangeae, represents a heterogeneous assembly of nine genera (*Broussaisia* Gaudich., *Cardiandra* Siebold & Zucc., *Decumaria* L., *Deinathe* Maxim., *Dichroa* Lour., *Hydrangea* L., *Pileostegia* Hook.f. & Thomson, *Platycrater* Siebold & Zucc., *Schizophragma* Siebold & Zucc.), encompassing warm temperate to tropical species (Table 1) with shrubby, herbaceous or root-climbing growth forms (Samain & al., 2010; Granados Mendoza & al., 2014; Fig. 1). Many representatives of this tribe have inflorescences with large, showy marginal flowers, to which these plants owe their popularity as garden ornamentals.

A small but representative sampling of Hydrangeae was included in studies addressing the evolutionary relationships within the Hydrangeaceae using both morphological (Hufford & al., 1997) and molecular (Soltis & al., 1995; Hufford & al., 2001) data. In addition to suffering from low statistical support, these studies resulted in different phylogenetic hypotheses. Sequencing a series of chloroplast regions for an extensive sampling of specimens, Samain & al. (2010) were able to identify two well-supported clades in tribe Hydrangeae. A first clade, termed Hydrangea I, contained *Cardiandra*, *Decumaria*, *Deinathe*, *Pileostegia*, *Schizophragma* and several representatives of *Hydrangea*. Relationships among these genera remained mainly unresolved. In the second major clade, termed Hydrangea II, *Broussaisia* and *Dichroa* were in a grade with two separate clades of *Hydrangea* representatives. Therefore, the results obtained by Samain & al. (2010) suggest that *Hydrangea* is a

polyphyletic assemblage, with the remaining eight genera of Hydrangeae phylogenetically nested within *Hydrangea*. Moreover, this study suggested that the infrageneric classification of *Hydrangea* proposed by McClintock (1957) is in need of revision. In a more recent study, Granados Mendoza & al. (2013) tested the utility of 13 plastid markers using a reduced sampling for resolving backbone relationships within tribe Hydrangeae (*Broussaisia* not included). A highly supported phylogenetic hypothesis was recovered for Hydrangea I and II, offering better resolution within the first clade, and only leaving the position of *H. arborescens* L. unsupported. Furthermore, *Hydrangea* was once more recovered as a polyphyletic assemblage, corroborating the findings by Samain & al. (2010).

In the present study, a comprehensive phylogeny of tribe Hydrangeae is presented, sampling all major evolutionary clades retrieved in previous studies, using four plastid markers selected according to their phylogenetic informativeness (Granados Mendoza & al., 2013) and ITS. Using the resulting phylogenetic hypothesis, we address the polyphyletic nature of *Hydrangea* and evaluate the merits of creating a monophyletic *Hydrangea*. Finally, a new infrageneric classification is proposed, incorporating the inferred relationships among and within subclades Hydrangea I and II. Throughout the manuscript, all section names used are those of the here-proposed classification of *Hydrangea* s.l., the broad circumscription of *Hydrangea*, including the other eight genera of tribe Hydrangeae. In contrast, *Hydrangea* s.str. refers to the previously recognized, polyphyletic *Hydrangea*, not including the eight satellite genera.

■ MATERIALS AND METHODS

Taxon sampling. — Taxa pertaining to all major clades and subclades recovered in Samain & al. (2010), all sections and subsections proposed in McClintock's (1957) infrageneric classification, as well as the eight allied genera *Broussaisia*, *Cardiandra*, *Decumaria*, *Deinathe*, *Dichroa*, *Pileostegia*, *Platycrater* and *Schizophragma* were sampled. For all genera

Table 1. Genera in tribe Hydrangeae, with number of published names and broad distribution, prior to merging the satellite genera into *Hydrangea*.

	Author	No. of species	Distribution
<i>Broussaisia</i>	Gaudich.	2	Hawaii
<i>Cardiandra</i>	Siebold & Zucc.	9	East Asia
<i>Decumaria</i>	L.	7	China, North America
<i>Deinathe</i>	Maxim.	2	East Asia
<i>Dichroa</i>	Lour.	23	East Asia
<i>Hydrangea</i> s.str.	L.	140	East and Southeast Asia, New World
<i>Pileostegia</i>	Hook.f. & Thomson	6	China, east India, Japan
<i>Platycrater</i>	Siebold & Zucc.	2	East Asia
<i>Schizophragma</i>	Siebold & Zucc.	17	East Asia
<i>Hydrangea</i> s.l.	L.	208	East and Southeast Asia, New World

Currently recognized number of species after merging indicated as *Hydrangea* s.l. in bold. Table with all currently recognized species names in the Electr. Suppl.: Table S1.

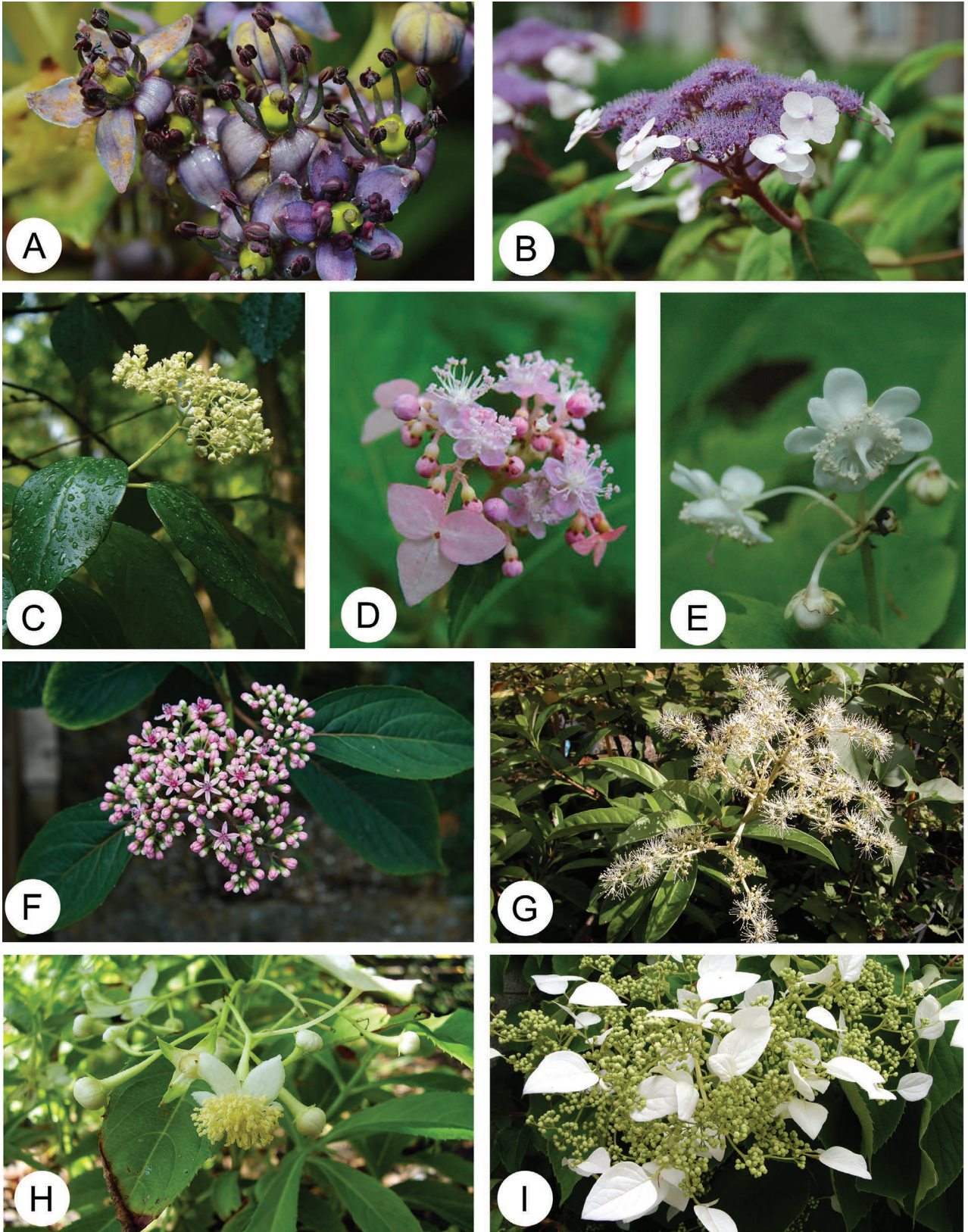


Fig. 1. Genera of tribe Hydrangeeae. **A**, *Broussaisia arguta* Gaudich.; **B**, *Hydrangea aspera* Buch.-Ham. ex D.Don.; **C**, *Decumaria barbara* L.; **D**, *Cardiandra alternifolia* (Siebold) Siebold & Zucc.; **E**, *Deinanthe bifida* Maxim.; **F**, *Dichroa febrifuga* Lour.; **G**, *Pileostegia viburoides* Hook.f. & Thomson; **H**, *Platycrater arguta* Siebold & Zucc.; **I**, *Schizophragma hydrangeoides* Siebold & Zucc. — Photo credits: A, J.T. Johansson; B, K. Bauters; C, J. McMillian; D, H. Moriyama; E, H. Arlen; F, W. Hagens; G, M. Laurent; H, G.E. Bush; I, <http://www.jardiplante.fr>

under study, a specimen representing the type was included. Two species of Loasaceae (*Loasa tricolor* Ker Gawl., *Xylopodia klaprothioides* Weigend) and two species of Hydrangeaceae tribe Philadelphaceae (*Philadelphus mexicanus* Schtdl., *Philadelphus pekinensis* Rupr.) were used as outgroups. Material used for DNA extraction consisted of silica-gel dried leaf tissue of wild collected accessions, while fresh leaves were used for material originating from botanical gardens.

Molecular methods and alignments. — Total genomic DNA was extracted from leaf tissue using a modified CTAB method (Doyle & Doyle, 1987). Four noncoding plastid regions, previously shown to be phylogenetically informative for tribe Hydrangeeae (Granados Mendoza & al., 2013), were utilized in this study. The *rpl32-ndhF* intergenic spacer (IGS), *trnV-ndhC* IGS, *trnL-rpl32* IGS and the *ndhA* intron were sequenced for all accessions. Primer sequences and protocols for PCR amplification were taken from Granados Mendoza & al. (2013), with the exception of the amplification of the *ndhA* intron for the *Asperae* clade, which required the design of the additional primers *ndhA-asp-F* (GATTCGTTGAGACATAAATT) and *ndhA-asp-R* (GTACATGAGATTTTCACCT). These plastid markers are non-overlapping and distributed across the large and short single copies of the chloroplast genome (Granados Mendoza & al., 2013). In order to rule out incorrect conclusions based on incongruence between plastid and nuclear phylogenies, ITS was sequenced for a subset of taxa, representing all major clades found in the plastid analyses. Sequencing of this region was performed using primers ITS1 and ITS4 with PCR conditions as described in White & al. (1990). Raw sequences were edited in Sequencher v.5.0.1 (Gene Codes Corporation), and aligned with Muscle v.3.8.1 (Edgar, 2004). The obtained alignments were subsequently evaluated manually, excluding regions of uncertain homology such as mononucleotide repeats (for a list of excluded regions, see Electr. Suppl.: Table S2). Insertions and deletions (indels) were coded following the simple indel coding scheme of Simmons & Ochoterena (2000) available in SeqState v.1.4.1 (Müller, 2005).

Phylogenetic analysis. — The most appropriate model for nucleotide evolution was selected with the Akaike information criterion (AIC) in jModelTest v.2.1.3 (Darriba & al., 2012). This procedure selected the TVM+G model for all regions except for the *trnL-rpl32* IGS, for which GTR+G was preferred. Bayesian inference analysis was run in MrBayes v.3.2.1 (Ronquist & al., 2012), for each of the four plastid regions and ITS separately, a concatenated matrix containing all four plastid regions, and a concatenated matrix combining the plastid regions with ITS. The concatenated dataset was generated to examine the impact of the information in the ITS dataset on the phylogenetic relationships recovered, and only attempted since there were no supported (posterior probability > 0.95) incongruences. For each of the above-mentioned alignments, two analyses were run; one with and one without indels coded. All analyses were run using the GTR+G model, since the TVM model is not implemented in MrBayes. The analyses of the concatenated matrices were run with partitions for each region, unlinking model parameters for each partition. The Markov Chain Monte Carlo (MCMC) was run using four simultaneous runs with four

chains each, for a total of five million generations, sampling trees every 100 generations. Parameter sampling was checked in Tracer v.1.6 (Rambaut & al., 2014) to ensure stationarity for each run. Discarding the first 12,500 trees as burn-in, the remaining trees were used to calculate the posterior probabilities (PP) of clades using the majority-rule consensus. The Cyber infrastructure for Phylogenetic Research (Cipres Science gateway; <http://www.phylo.org>; Miller & al., 2010) was used to run all Bayesian analyses. A maximum likelihood analysis in RAxML v.7.2.8 (Stamatakis & al., 2005) was performed on both concatenated datasets (plastid and plastid+ITS) without indel coding, using the GTRGAMMA model for sequence evolution, with the dataset partitioned according to marker regions, and 1000 rapid bootstrap replicates (Stamatakis & al., 2008).

Phylogenetic hypothesis testing. — Bayesian phylogenetic inference did not resolve the evolutionary position of three taxa: *Broussaisia arguta* Gaudich., *Hydrangea arbore-scens* and *H. quercifolia* W.Bartram. Therefore, all possible resolutions of the unsupported branches in the phylogenetic hypothesis were statistically compared using Bayesian inference and the combined plastid dataset with indels coded. The marginal likelihoods for each possible resolution were calculated using the stepping stone algorithm (Xie & al., 2011), as implemented in MrBayes v.3.2.2 (Ronquist & al., 2012). For each hypothesis under study, a phylogenetic tree with all major clades constrained to match the phylogenetic hypothesis was used as a prior, in accordance with the preferred approach of Bergsten & al. (2013). The stepping stone algorithm was run for 10 million generations over 50 steps, with the first step as burn-in for four independent runs. The marginal likelihoods for each hypothesis were then compared using Bayes Factors (Kass & Raftery, 1995).

Estimating phylogenetic informativeness. — The online application PhyDesign (López-Giráldez & Townsend, 2011) was used to calculate the net phylogenetic informativeness (Townsend, 2007) for each marker used in this study. This calculation used an ultrametric tree generated from the combined plastid and ITS dataset without indel coding. Substitution rates were estimated in HyPhy v.2.2.1 (Pond & al., 2005). Phylogenetic informativeness profiles for each individual region were compared to the reference ultrametric tree. Maximum net phylogenetic informativeness (PI_{max}) was documented for each separate region, in order to determine the point in time at which each region is phylogenetically most informative.

■ RESULTS

Data matrices. — Final alignments for the plastid regions contained 1704, 1553, 1188, 1283 and 664 nucleotide characters for the *rpl32-ndhF* IGS, *trnV-ndhC* IGS, *trnL-rpl32* IGS, *ndhA* intron and ITS region, respectively. Simple indel coding (Simmons & Ochoterena, 2000) resulted in the addition of 112, 90, 76, 72 and 53 binary characters, respectively. The *trnV-ndhC* IGS for *Broussaisia arguta* contained two unique deletions of 169 and 1062 bp, respectively. These deletions were confirmed by resequencing both accessions twice.

Phylogenetic inference. — In the plastid combined analysis (concatenated chloroplast nucleotide dataset, including indel data; Fig. 2), *Hydrangea* sect. *Dichroa* is sister to a grade of the monophyletic sect. *Macrophyllae*, sect. *Hirtae* and sect. *Chinenses*. *Hydrangea* sect. *Stylosae* is recovered as sister to this entire assemblage, completing a clade congruent with Hydrangea II without *Broussaisia arguta*. This latter taxon is sister to a strongly supported clade (PP: 1) coinciding with Hydrangea I. This sister relationship, however, remains weakly supported (PP: 0.61). Within Hydrangea I, *H. arborescens* and *H. quercifolia* are grouped in a weakly supported clade

(PP: 0.52), and are sister to the rest of Hydrangea I. In this major clade, sect. *Pileostegia* is sister to a clade containing the monophyletic sections *Schizophragma* and *Decumaria*, while sect. *Heteromallae* is sister to this entire assemblage (PP: 0.7). *Hydrangea* sect. *Cardiandra* is recovered as monophyletic and in a sister relationship with a monophyletic sect. *Deinanthe*, while this assemblage is sister to the clade comprising sections *Heteromallae*, *Schizophragma*, *Decumaria* and *Pileostegia*. All these sections are in turn sister to a clade containing sects. *Asperae*, *Cornidia*, *Calyptanthe* and *Platycrater arguta*. The last is phylogenetically nested within sect. *Asperae*, which

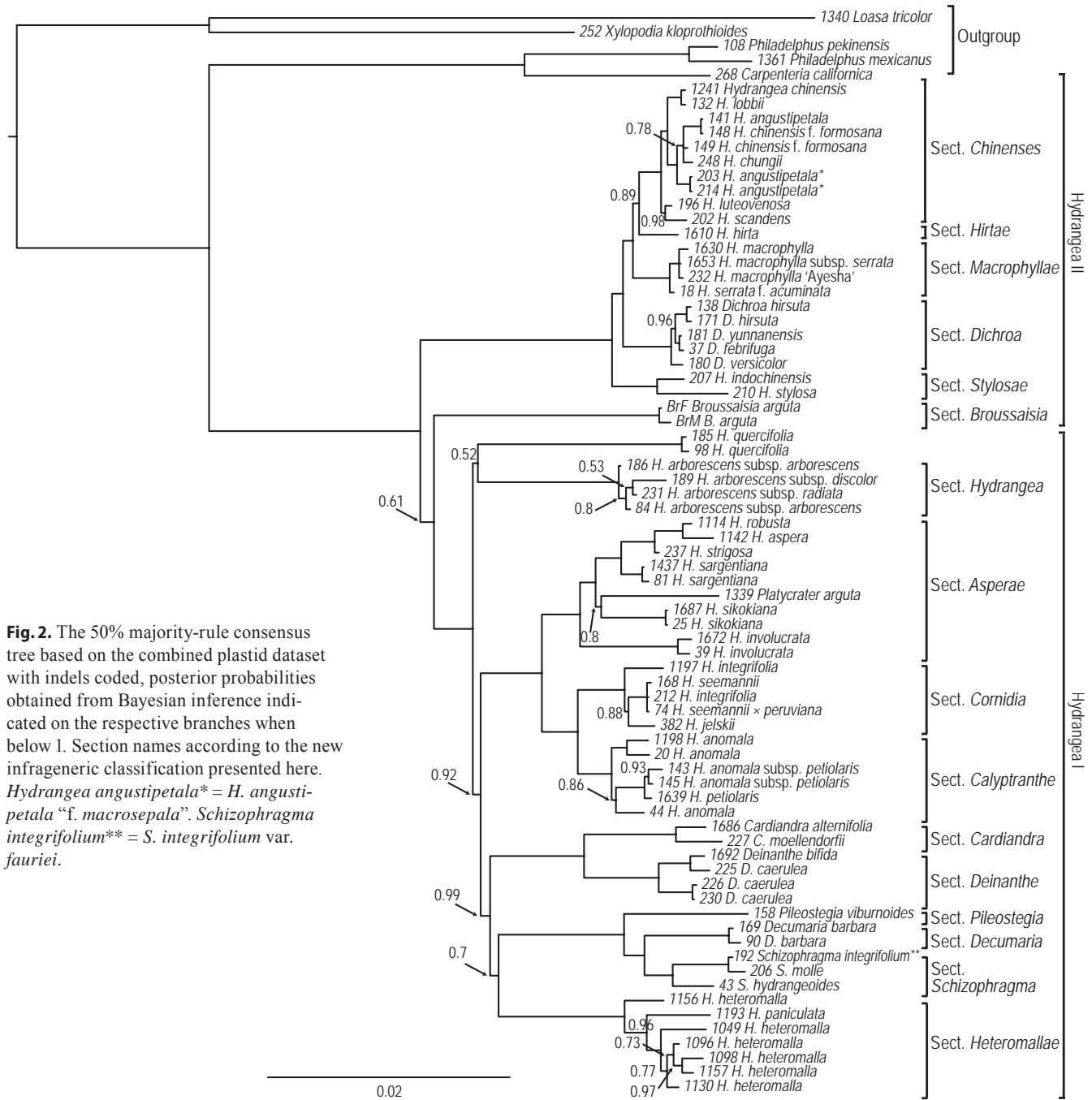


Fig. 2. The 50% majority-rule consensus tree based on the combined plastid dataset with indels coded, posterior probabilities obtained from Bayesian inference indicated on the respective branches when below 1. Section names according to the new infrageneric classification presented here. *Hydrangea angustipetala** = *H. angustipetala* “f. *macrosepala*”. *Schizophragma integrifolium*** = *S. integrifolium* var. *fauriei*.

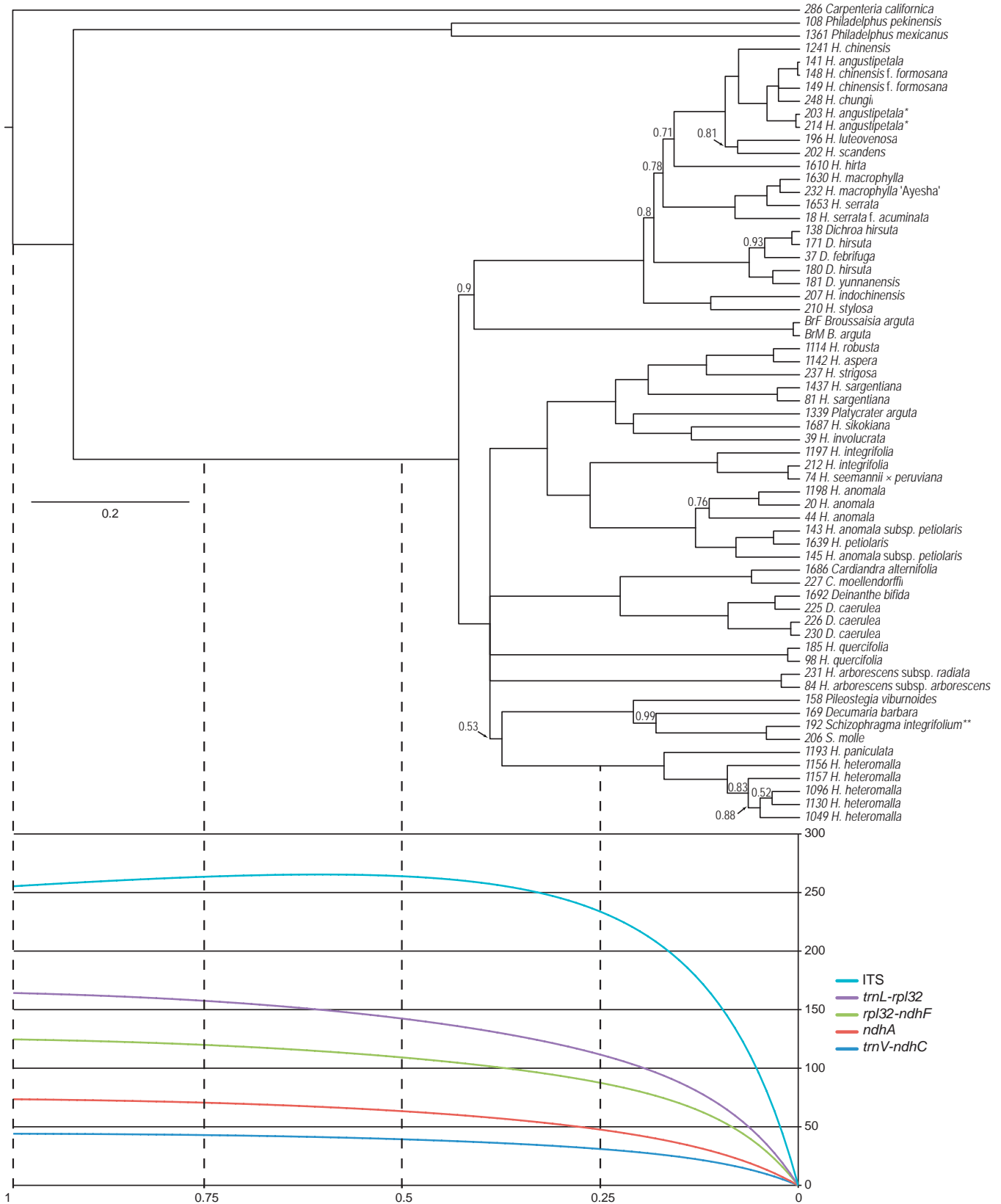


Fig. 3. Net phylogenetic informativeness across time for all four sequenced regions, plotted against the ultrametric phylogenetic tree based on ITS and plastid sequences, excluding indel data. Posterior probabilities for branches only displayed if below 1. *Hydrangea angustipetala** = *H. angustipetala* “f. *macrosepala*”. *Schizophragma integrifolium*** = *S. integrifolium* var. *fauriei*.

in turn is sister (PP: 1) to a clade (PP: 1) containing the two highly supported monophyletic sister sections *Cornidia* and *Calyptranthe*. Analysis of the indel-coded concatenated dataset including the ITS region recovered a similar phylogenetic hypothesis, the only topological difference being the position of *Broussaisia arguta*. This taxon is sister to a well-supported clade (PP: 1) consisting of sect. *Chinenses*, sect. *Hirtae*, sect. *Macrophyllae*, sect. *Dichroa* and sect. *Stylosae*. Furthermore, support for the deeper nodes is reduced by adding ITS to the analysis (Fig. 3).

Including the data from the simple indel coding scheme generally improved clade support in the Bayesian analysis for the separate regions. Topology was not affected by inclusion of these characters, except for the position of *Broussaisia arguta* in the analysis of the *rpl32-ndhF* IGS and the concatenated dataset (Electr. Suppl.: Figs. S1, S2). For the *rpl32-ndhF* region, *B. arguta* was sister to the Hydrangea II clade with weak support (PP: 0.82) when only nucleotide data were analyzed (not shown), while this relationship was not recovered when indel data were added to the analysis (Electr. Suppl.: Figs. S2–S6). A parallel pattern for this taxon occurred in the combined plastid analysis, with *B. arguta* sister to Hydrangea II for the nucleotide data (PP: 0.80; Electr. Suppl.: Fig. S1), and sister to Hydrangea I (PP: 0.61) when indel data were included in the analysis (Fig. 2). Bayesian analysis of the datasets combining plastid and ITS data recovered *B. arguta* as sister to Hydrangea II (PP: 0.90, not shown) when indels were not coded, while this

relationship was not supported when indels were coded (PP: 0.67, Fig. 3).

Analyses of separate regions did not yield well-supported conflicts. The position of *H. arborescens* and *H. quercifolia* remains unresolved in all single-gene trees and the combined analyses. However, these taxa are recovered as part of a well-supported clade with the representatives of Hydrangea I in the combined analyses (with and without indel data, Figs. 2, 3 and Electr. Suppl.: Fig. S1) and the single gene trees for *rpl32-ndhF* IGS and *trnV-ndhC* IGS (Electr. Suppl.: Figs. S2, S3). Phylogenetic hypotheses resulting from the ML analyses did not show any supported topological differences with those generated with Bayesian inference (Electr. Suppl.: Fig. S7).

Hypothesis testing. — Comparing the marginal likelihoods obtained from the stepping stone algorithm for each of the nine hypotheses (Fig. 4) showed four hypotheses (M3–M6) to be strongly preferred over the alternatives (Table 2). Models placing *Broussaisia arguta* sister to the rest of Hydrangea II are preferred over alternative models with the same configuration for *H. arborescens* and *H. quercifolia*. Between models sharing the same placement of *B. arguta* (Fig. 4A–C, D–F and G–I), the model placing *H. quercifolia* sister to the rest of Hydrangea I shows the highest marginal likelihood. Bayes Factor analysis only shows this difference to be strongly supported for model M3 over M2 and M1, and for M9 over M8 and M7.

Phylogenetic informativeness. — The phylogenetic informativeness profiles of all sequenced regions are plotted below

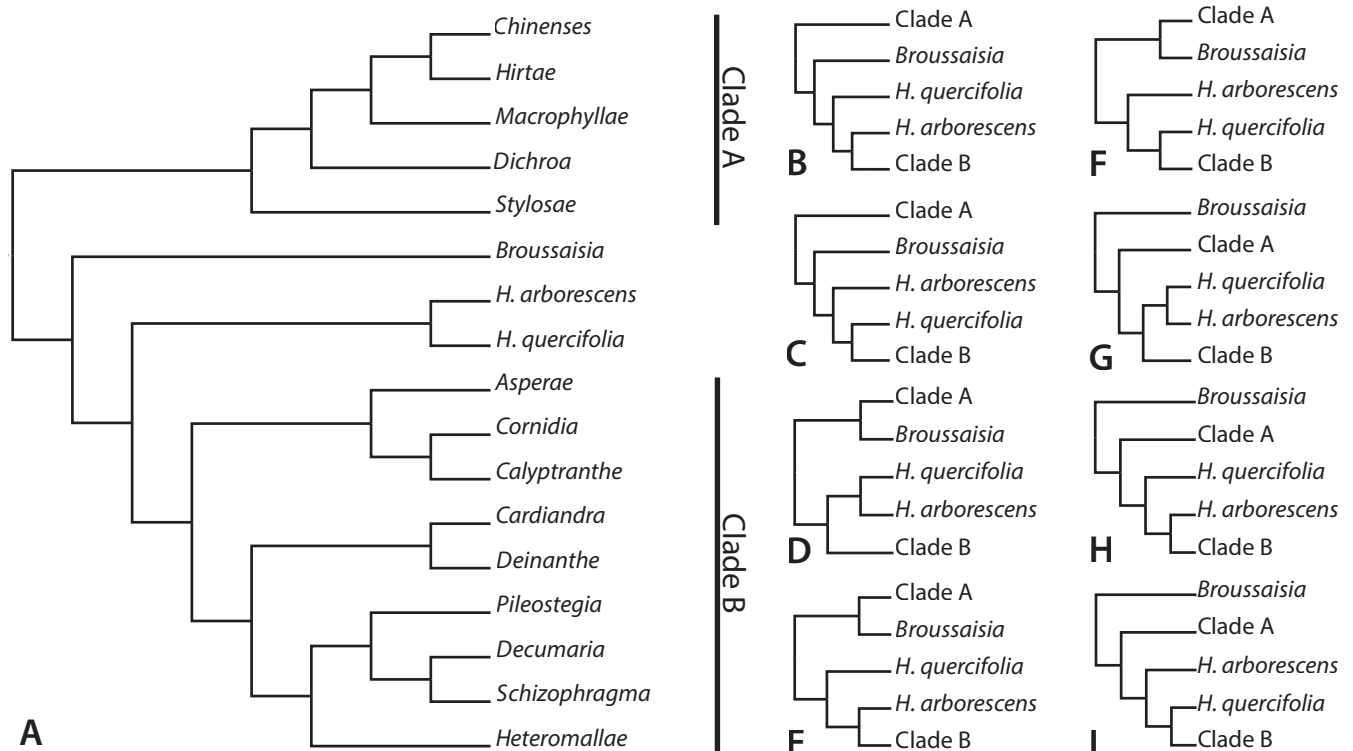


Fig. 4. Phylogenetic hypothesis used for Bayesian hypothesis testing. **A**, The full tree corresponding to model M1, monophyly of all sections was constrained, as were all depicted nodes. **B–I**, alternative hypotheses, clade A and B are constrained as depicted in Fig. 4A, positions of *Broussaisia*, *H. quercifolia* and *H. arborescens* differ between models (B: model M2, C: model M3, D: model M4, E: model M5, F: model M6, G: model M7, H: model M8, I: model M9).

the ultrametric tree based on the concatenated dataset with ITS and plastid regions, without indel coding in Fig. 3. The profile for the ITS region reaches a clear maximum at time 0.35, which is prior to the divergence of tribe Hydrangeeae at time 0.43, and sharply declines towards more ancient times. The plastid regions show lower, flatter profiles, steadily increasing in informativeness towards deeper nodes. Of the plastid regions, the *rpl32-ndhF* IGS reaches the highest informativeness, followed by *trnV-ndhC*, *trnL-rpl32* intergenic spacers and finally the *ndhA* intron, respectively.

DISCUSSION

Generic relationships, congruences and conflicts in tribe Hydrangeeae. — This study presents the most comprehensive phylogenetic hypothesis for tribe Hydrangeeae to date. Single gene trees for the ITS region (Electr. Suppl.: Fig. S6) showed the same major clades as the chloroplast markers. Resolution for the deeper nodes remained much lower than in the combined plastid analysis. Furthermore, inclusion of ITS into the concatenated analysis drastically reduced support for evolutionary relationships among large clades (sections) within Hydrangea I (Fig. 3). The inclusion of the ITS data therefore introduced noise into the dataset, as can be deduced from the phylogenetic informativeness profile in Fig. 3. The maximum phylogenetic informativeness of ITS is reached more recently ($t = 0.35$) than the divergence of the major clades in Hydrangea I. This region was therefore fairly uninformative for resolving evolutionary relationships prior to this time, as more recent changes in its sequence might obscure signals that have arisen within the time interval of the divergence of these major Hydrangea I lineages (Townsend, 2007). The more uniform informativeness profiles of the plastid markers, the better suited they are for resolving deeper nodes in tribe Hydrangeeae. Consequently, the new classification presented here is discussed using the phylogenetic tree based on the concatenated chloroplast regions (Fig. 2), as this is the most complete dataset, with best support for relationships among sections. In this phylogenetic hypothesis,

the morphologically diverse genera *Broussaisia*, *Cardiandra*, *Decumaria*, *Deinanthe*, *Dichroa*, *Pileostegia*, *Platycrater* and *Schizophragma* were recovered as monophyletic, but nested within the larger polyphyletic *Hydrangea* (Fig. 2). These findings were in general agreement with earlier studies (Samain & al., 2010; Granados Mendoza & al., 2013). A combined analysis of 13 chloroplast regions by Granados Mendoza & al. (2013) recovered *H. quercifolia* in a grade with *H. arborescens* and a clade containing sect. *Asperae* (plus *Platycrater*) as sister to the sister sections *Calyptranthe* and *Cornidia*. The short branch subtending *H. arborescens*, however, remained unsupported in Granados Mendoza & al. (2013). In the present study, phylogenetic placement of *H. arborescens* and *H. quercifolia* was only partly resolved (with low support) for the combined plastid dataset with indels coded and both analyses of the *rpl32-ndhF* IGS (Electr. Suppl.: Fig. S2). Furthermore, the Bayesian test of phylogenetic hypotheses did not prefer one configuration of these taxa over alternative configurations. The reason for this absence of resolution is the presence of deep, short branches connecting the two North American taxa to the rest of the tribe, combined with long branches subtending these monophyletic species. Resolving such short branches positioned deep in a phylogeny is considered a difficult endeavour (Townsend & Leuenberger, 2011), and requires multiple genes of high phylogenetic signal and demonstrated absence of incongruence (Salichos & Rokas, 2013), or loci highly informative on that specific time scale (Townsend, 2007). Moreover, resolving the position of *H. arborescens* is of pivotal importance as this taxon is the type of *Hydrangea*.

A second conflict between the present and previous studies was the position of the Hawaiian endemic *Broussaisia arguta*. The phylogenetic hypothesis generated by Samain & al. (2010) placed this taxon sister to Hydrangea II with high support (bootstrap: 96, PP: 0.98). The current study, however, recovered a weakly supported sister relationship (PP: 0.61, Fig. 2) between *B. arguta* and Hydrangea I in the plastid concatenated analysis incorporating indel data, while *B. arguta* was sister to Hydrangea II (PP: 0.80) when indels were not coded (Electr. Suppl.: Fig. S1). When ITS was added to the concatenated

Table 2. Comparison of the nine different hypotheses presented in Fig. 4 using Bayes factors.

	M1	M2	M3	M4	M5	M6	M7	M8	M9
M1	1.00	12.68	0.01	0.02	0.02	0.01	34.47	32.79	1.27
M2	0.08	1.00	0.00	0.00	0.00	0.00	2.72	2.59	0.10
M3	79.84	1012.32	1.00	1.23	1.62	0.51	2751.77	2617.57	101.49
M4	64.72	820.57	0.81	1.00	1.31	0.41	2230.54	2121.76	82.27
M5	49.40	626.41	0.62	0.76	1.00	0.32	1702.75	1619.71	62.80
M6	156.02	1978.31	1.95	2.41	3.16	1.00	5377.61	5115.34	198.34
M7	0.03	0.37	0.00	0.00	0.00	0.00	1.00	0.95	0.04
M8	0.03	0.39	0.00	0.00	0.00	0.00	1.05	1.00	0.04
M9	0.79	9.97	0.01	0.01	0.02	0.01	27.11	25.79	1.00

Bayes factors calculated with the stepping stone algorithm for comparison of the nine alternative phylogenetic hypotheses (M1–M9) presented in Fig. 4. Values >3 but <10 signify strong support for H1 over H2, values >10 signify strong support for H1 over H2, in which H1 is the model in the first column, H2 the model in the top row (Jeffreys, 1961).

dataset, *B. arguta* was recovered as sister to Hydrangea II whether or not indel data were included, although higher support was achieved with the inclusion of indel data (PP: 0.90; Fig. 3). Comparison of marginal likelihoods for the different positions of *B. arguta* (Fig. 2; Table 2) preferred the sister relationship with Hydrangea II over the alternative positions, which is congruent with the results shown in Samain & al. (2010). The contrasting position of *B. arguta* in the phylogenetic analysis of the concatenated data with indels coded might therefore be heavily influenced by the presence of large indels within the *trnV-ndhC* IGS. The long branches subtending this species might indicate an accelerated rate of molecular change, obscuring the evolutionary relationships of *Broussaisia*. A similar pattern was recovered in the Cornales family Hydrostachyaceae (Xiang & al., 1998; Xiang Q.Y., 1999; Fan & Xiang, 2003; Xiang X.G. & al., 2012), where the difficulties of reconstructing relationships in this group were suggested to be caused by an acceleration of evolution in molecular and morphological characters. Shifts into novel environments, followed by selection, increased mutation rates and genetic drift were suggested as likely to have caused this accelerated accumulation of variation. Similarly, the long branches subtending *B. arguta*, as well as its deviating molecular sequences might be caused by its isolated geographic location, as the only member of tribe Hydrangeeae endemic to the Hawaiian Islands.

From a polyphyletic *Hydrangea* s.str. to a monophyletic *Hydrangea* s.l. — Unraveling the polyphyletic nature of *Hydrangea* is a necessity, as neither of the large schools of systematics accepts polyphyletic taxa (Hörandl & Stuessy, 2010; Schmidt-Lebuhn, 2012). Phylogenetic hypotheses resulting from the present study suggest two possible resolutions: (1) creating new genera to accommodate monophyletic groups of *Hydrangea* not directly related to the type *H. arborescens*, retaining the eight satellite genera as separate entities, or, (2) including the eight satellite genera into *Hydrangea*, creating a broadly circumscribed, monophyletic *Hydrangea* s.l. The first approach would entail splitting *Hydrangea*, with the description of minimally seven new genera, of which two would be monotypic. Furthermore, splitting *Hydrangea* s.str. would result in morphologically very similar taxa which would be very difficult to distinguish. Several degrees of splitting can be proposed, depending on the acceptance of monotypic and paraphyletic genera. For example, in order to retain the genus *Platycrater*, McClintock's subsect. *Asperae* would have to be split into three genera, two of them monotypic. The second approach entails the creation of a large genus *Hydrangea*, containing all species of the eight satellite genera, among which several taxa would require new specific epithets. Furthermore, the newly created *Hydrangea* s.l. would display wide variation in morphology, losing the practicability of classifying morphologically aberrant taxa as separate (satellite) genera.

It is argued here that a splitting approach, creating several new genera, would complicate Hydrangeeae taxonomy, resulting either in a large amount of monotypic genera or multiple morphologically very variable, and hence potentially unrecognizable, taxa. Furthermore, small changes in relationships between clades potentially recovered in future studies may

possibly require new changes in number and configuration of genera. Therefore, a broad circumscription of *Hydrangea* to include *Broussaisia*, *Cardiandra*, *Decumaria*, *Deinathe*, *Dichroa*, *Pileostegia*, *Platycrater* and *Schizophragma* would best serve the science of taxonomy, in creating a stable classification.

We do recognize the point made by evolutionary systematists that a classification should carry information about similarities between its constituents. Therefore, a new infrageneric classification is proposed, which is expected to facilitate the acceptance of the taxonomical changes in horticulture. By circumscribing the previous satellite genera as distinct sections, these entities remain recognizable for the broader public, with already well-known names, albeit at a different taxonomic level.

■ TAXONOMIC TREATMENT

- Hydrangea* L., Sp. Pl.: 397. 1753 – Type: *H. arborescens* L.
 = *Decumaria* L., Sp. Pl., ed. 2: 1663. 1763 – Type: *D. barbara* L.
 = *Dichroa* Lour., Fl. Cochinch.: 301. 1790 – Type: *D. febrifuga* Lour.
 = *Broussaisia* Gaudich., Voy. Uranie: 479. 1830 – Type: *B. arguta* Gaudich.
 = *Schizophragma* Siebold & Zucc., Fl. Jap. 1: 58. 1838 – Type: *S. hydrangeoides* Siebold & Zucc.
 = *Platycrater* Siebold & Zucc., Fl. Jap. 1: 62. 1838 – Type: *P. arguta* Siebold & Zucc.
 = *Cardiandra* Siebold & Zucc., Fl. Jap. 1: 119. 1839 – Type: *C. alternifolia* (Siebold) Siebold & Zucc.
 = *Pileostegia* Hook.f. & Thomson in J. Proc. Linn. Soc., Bot. 2: 57. 1857 – Type: *P. viburnoides* Hook.f. & Thomson.
 = *Deinathe* Maxim. in Mém. Acad. Imp. Sci. Saint Pétersbourg, ser. 7, 10(16): 2. 1867 – Type: *D. bifida* Maxim.

A new infrageneric classification of *Hydrangea*, including new sections and combinations. — The eight satellite genera of *Hydrangea* are recognized as distinct sections, with the exception of *Platycrater*, which is placed in sect. *Asperae* in order to avoid the creation of a polyphyletic *Asperae*. The subsections in the classification of McClintock (1957) are raised to section level. Assignment of all currently recognized Hydrangeeae species names to their respective section is provided in Electr. Suppl.: Table S1.

1. *Hydrangea* sect. *Asperae* (Rehder) Y.De Smet & Samain, **stat. nov.** ≡ *H.* subsect. *Asperae* Rehder in Sargent, Pl. Wilson. 1: 39. 1911 – Type: *H. aspera* D. Don.

Hydrangea platyarguta Y.De Smet & Granados, **nom. nov.** ≡ *Platycrater arguta* Siebold & Zucc., Fl. Jap. 1: 62, t. 64. 1835, non *Hydrangea arguta* (Gaudich.) Y.De Smet & Granados (see below).

2. *Hydrangea* sect. *Broussaisia* (Gaudich.) Y.De Smet & Samain, **comb. & stat. nov.** ≡ *Broussaisia* Gaudich., Voy.

- Uranie: 479. 1830 – Type: *Hydrangea arguta* (Gaudich.) Y.De Smet & Granados.
- Hydrangea arguta*** (Gaudich.) Y.De Smet & Granados, **comb. nov.** ≡ *Broussaisia arguta* Gaudich., Voy. Uranie: 479, t. 69. 1830.
3. ***Hydrangea*** sect. ***Calyptranthe*** Maxim. in Mém. Acad. Imp. Sci. Saint Pétersbourg, ser. 7, 10(16): 6. 1867 – **Type (designated here):** *H. scandens* Maxim. in Mém. Acad. Imp. Sci. Saint Pétersbourg, ser. 7, 10(16): 16. 1867.
Maximowicz assigned two species to this section; *Hydrangea scandens* Maxim. (newly described) and *H. altissima* Wallich (with a short note). Both names are now considered synonyms of *Hydrangea anomala* D.Don 1825 s.l.
4. ***Hydrangea*** sect. ***Cardiandra*** (Siebold & Zucc.) Y.De Smet & Samain, **comb. & stat. nov.** ≡ *Cardiandra* Siebold & Zucc., Fl. Jap. 1: 119. 1839 – Type: *Hydrangea alternifolia* Siebold in Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 14(2): 692. 1829.
- Hydrangea amamiohsimensis*** (Koidz.) Y.De Smet & Granados, **comb. nov.** ≡ *Cardiandra amamiohsimensis* Koidz., Pl. Nov. Amami-Ohsim: 10. 1928.
- Hydrangea densifolia*** (C.F.Weil) Y.De Smet & Granados, **comb. nov.** ≡ *Cardiandra densifolia* C.F.Weil. in Acta Bot. Austro Sin. 10: 9, fig. 1. 1995.
= *Cardiandra formosana* Hayata in Bot. Mag. (Tokyo) 20: 54–55. 1906, non *Hydrangea formosana* Koidz. in Bot. Mag. (Tokyo) 43: 394. 1929.
5. ***Hydrangea*** sect. ***Chinenses*** Y.De Smet & Samain, **sect. nov.** – Type: *H. chinensis* Maxim. in Mém. Acad. Imp. Sci. Saint Pétersbourg, ser. 7, 10(16): 7. 1867.
= *Hydrangea* sect. ***Petalanthae*** Maxim. in Mém. Acad. Imp. Sci. Saint Pétersbourg, ser. 7, 10(16): 6. 1867, nom. illeg. (Art. 22.2).
Small shrubs with rather small and narrow leaves, inflorescences rather numerous, scattered over many branchlets, with enlarged marginal flowers.
Hydrangea sect. ***Petalanthae*** as proposed by Maximowicz (1867) is illegitimate, as it contains the type of *Hydrangea*. Here this section is renamed as sect. ***Chinenses***.
6. ***Hydrangea*** sect. ***Cornidia*** (Ruiz & Pav.) Engl., Nat. Pflanzenfam. 3(2a): 76. 1891 ≡ *Cornidia* Ruiz & Pav., Fl. Peruv. Prodr.: 53, pl. 35. 1794 – Type: *Hydrangea preslii* Briq. in Annuaire Conserv. Jard. Bot. Genève 20: 409–410. 1919.
7. ***Hydrangea*** sect. ***Decumaria*** (L.) Y.De Smet & Samain, **comb. & stat. nov.** ≡ *Decumaria* L., Sp. Pl., ed. 2: 1663. 1763 – Type: *Hydrangea barbara* (L.) B.Schulz, Gehölzbestimmung Winter: 285. 2013.
- Hydrangea obtusifolia*** (Hu) Y.De Smet & Granados, **comb. nov.** ≡ *Schizophragma obtusifolium* Hu in Bull. Fan Mem. Inst. Biol. 5: 309. 1934
= *Decumaria sinensis* Oliv. in Hooker's Icon. Pl. 18: pl. 1741. 1888, non *Hydrangea chinensis* Maxim. in Mém. Acad. Imp. Sci. Saint Pétersbourg, ser. 7, 10(16): 7. 1867.
8. ***Hydrangea*** sect. ***Deinanthe*** (Maxim.) Y.De Smet & Samain, **comb. & stat. nov.** ≡ *Deinanthe* Maxim. in Mém. Acad. Imp. Sci. Saint Pétersbourg, ser. 7, 10(16): 2. 1867 – Type: *Hydrangea bifida* (Maxim.) Y.De Smet & Granados.
- Hydrangea bifida*** (Maxim.) Y.De Smet & Granados, **comb. nov.** ≡ *Deinanthe bifida* Maxim. in Mém. Acad. Imp. Sci. Saint Pétersbourg, ser. 7, 10(16): 3. 1867.
- Hydrangea caerulea*** (Stapf) Y.De Smet & Granados, **comb. nov.** ≡ *Deinanthe caerulea* Stapf in Bot. Mag. 137, t. 8373. 1911.
9. ***Hydrangea*** sect. ***Dichroa*** (Lour.) Y.De Smet & Samain, **comb. & stat. nov.** ≡ *Dichroa* Lour., Fl. Cochinch.: 301. 1790 – Type: *Hydrangea febrifuga* (Lour.) Y.De Smet & Granados.
- Hydrangea daimingshanensis*** (Y.C.Wu) Y.De Smet & Granados, **comb. nov.** ≡ *Dichroa daimingshanensis* Y.C.Wu in Bot. Jahrb. Syst. 71(2): 179. 1940.
- Hydrangea febrifuga*** (Lour.) Y.De Smet & Granados, **comb. nov.** ≡ *Dichroa febrifuga* Lour., Fl. Cochinch.: 301. 1790.
- Hydrangea hirsuta*** (Gagnep.) Y.De Smet & Granados, **comb. nov.** ≡ *Dichroa hirsuta* Gagnep. in Lecomte, Fl. Indo-Chine 2: 690. 1920.
- Hydrangea mollissima*** (Merr.) Y.De Smet & Granados, **comb. nov.** ≡ *Dichroa mollissima* Merr. in Philipp. J. Sci. 23: 245. 1923.
- Hydrangea yaoshanensis*** (Y.C.Wu) Y.De Smet & Granados, **comb. nov.** ≡ *Dichroa yaoshanensis* Y.C.Wu in Bot. Jahrb. Syst. 71(2): 180. 1940.
10. ***Hydrangea*** sect. ***Heteromallae*** (Rehder) C.F.Weil in Guihaia 14(2): 111. 1994 ≡ *Hydrangea* subsect. ***Heteromallae*** Rehder in Sargent, Pl. Wilson. 1: 37. 1911 – Type: *H. heteromalla* D.Don, Prodr. Fl. Nepal.: 211. 1825.
11. ***Hydrangea*** sect. ***Hirtae*** Y.De Smet & Samain, **sect. nov.** – Type: *H. hirta* (Thunb.) Siebold in Flora 11: 757. 1828 ≡ *Viburnum hirtum* Thunb., Fl. Jap.: 124. 1784.
Small shrubs with conspicuously dentate leaves, inflorescence a compact corymb, on a short peduncle, and enlarged marginal flowers absent.
12. ***Hydrangea*** sect. ***Hydrangea*** – Type: *H. arborescens* L., Sp. Pl.: 397. 1753.

The type of *Hydrangea*, *H. arborescens*, was classified in subsect. *Americanae* (Maxim.) Engl. (McClintock, 1957), together with another North American species, *H. quercifolia*. In this classification, sect. *Hydrangea* only consists of the morphologically very variable *H. arborescens*, while *H. quercifolia* remains unclassified. The latter is due to the unresolved relationships of this taxon in all phylogenetic hypotheses published to date.

13. *Hydrangea* sect. *Macrophyllae* (E.M.McClint.) Y.De Smet & Samain, **stat. nov.** ≡ *H.* subsect. *Macrophyllae* E.M.McClint. in J. Arnold Arbor. 37: 374. 1956 – Type: *H. macrophylla* (Thunb.) Ser. in Candolle, Prodr. 4: 15. 1830 ≡ *Viburnum macrophyllum* Thunb., Fl. Jap.: 125. 1784. In accordance with previous studies (Samain & al., 2010), subsect. *Macrophyllae* as recognized by McClintock (1957) was recovered here as polyphyletic, forming two well-supported clades. The clade containing *Hydrangea macrophylla* will remain as *Macrophyllae*, raised from subsection to section level. For the other clade, containing *H. indochinensis* and *H. stylosa*, a new name is provided (see below).

14. *Hydrangea* sect. *Pileostegia* (Hook.f. & Thomson) Y.De Smet & Samain, **comb. & stat. nov.** ≡ *Pileostegia* Hook.f. & Thomson in J. Proc. Linn. Soc., Bot. 2: 57. 1857 – Type: *Hydrangea viburnoides* (Hook.f. & Thomson) Y.De Smet & Granados.

Hydrangea tomentella (Hand.-Mazz.) Y.De Smet & Granados, **comb. nov.** ≡ *Pileostegia tomentella* Hand.-Mazz. in Anz. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 59: 55. 1922.

Hydrangea viburnoides (Hook.f. & Thomson) Y.De Smet & Granados, **comb. nov.** ≡ *Pileostegia viburnoides* Hook.f. & Thomson in J. Proc. Linn. Soc. 2: 76, pl. 2. 1857.

15. *Hydrangea* sect. *Schizopragma* (Siebold & Zucc.) Y.De Smet & Samain, **comb. & stat. nov.** ≡ *Schizopragma* Siebold & Zucc., Fl. Jap. 1: 58. 1838 – Type: *Hydrangea hydrangeoides* (Siebold & Zucc.) B.Schulz, Gehölzbestimmung Winter: 285. 2013 ≡ *Schizopragma hydrangeoides* Siebold & Zucc., Fl. Jap. 1: 59, pl. 26. 1835.

Hydrangea ampla (Chun) Y.De Smet & Granados, **comb. nov.** ≡ *Schizopragma amplum* Chun in Acta Phytotax. Sin. 3: 165–166. 1954.
= *Schizopragma integrifolium* Oliv. in Hooker's Icon. Pl. 20: pl. 1934. 1890, non *Hydrangea integrifolia* Hayata in J. Coll. Sci. Imp. Univ. Tokyo 22: 131. 1906.

Hydrangea corylifolia (Chun) Y.De Smet & Granados, **comb. nov.** ≡ *Schizopragma corylifolium* Chun in Acta Phytotax. Sin. 3: 170–172, pl. 21. 1954.

Hydrangea crassa (Hand.-Mazz.) Y.De Smet & Granados, **comb. nov.** ≡ *Schizopragma crassum* Hand.-Mazz. in Anz. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 59: 247. 1922.

Hydrangea fauriei (Hayata) Y.De Smet & Granados, **comb. nov.** ≡ *Schizopragma fauriei* Hayata in J. Coll. Sci. Imp. Univ. Tokyo 22: 131. 1906.

Hydrangea glaucescens (Rehder) Y.De Smet & Granados, **comb. nov.** ≡ *Schizopragma glaucescens* (Rehder) Chun in Acta Phytotax. Sin. 3: 166. 1954 ≡ *Schizopragma integrifolium* var. *glaucescens* Rehder in Sargent, Pl. Wilson. 1: 42. 1911.
= *Schizopragma hypoglaucum* Rehder in Sargent, Pl. Wilson. 1: 43. 1911, non *Hydrangea hypoglauca* Rehder in Sargent, Pl. Wilson. 1: 26. 1911.

Hydrangea schizomollis Y.De Smet & Granados, **nom. nov.** ≡ *Schizopragma integrifolia* var. *molle* Rehder in Sargent, Pl. Wilson. 1: 42. 1911, non *Hydrangea mollis* (Rehder) W.T.Wang in Bull. Bot. Res., Harbin 1(1–2): 54. 1981 ≡ *H. heteromalla* var. *mollis* Rehder in Sargent, Pl. Wilson. 1: 151. 1912.

16. *Hydrangea* sect. *Stylosae* Y.De Smet & Samain, **sect. nov.** – Type: *H. stylosa* Hook.f. & Thomson in J. Proc. Linn. Soc., Bot. 2: 75. 1857.

Small shrubs with rather small and narrow leaves, inflorescences with enlarged marginal flowers, their sepals conspicuously dentate, capsules globose, with usually four prominent styles.

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Appendix 1. Specimens analyzed in the phylogenetic analyses and Bayesian hypothesis testing. For each specimen, the species name and taxonomic authority is given, followed by the country of origin (if available), year of collection, collector and collector number and herbarium code, EMBL nucleotide sequence database accession numbers for the *ndhA* intron, *rpl32-ndhF* IGS, *trnL-rpl32* IGS, *trnV-ndhC* IGS and ITS respectively. An asterisk indicates new sequences.

Broussaisia: *B. arguta* Gaudich., Hawaii, 2014, *Walsh & al. W001* (GENT W001), LN830487*, LN830562*, LN830637*, LN830343*, LN830391* **B. arguta**, Hawaii, 2014, *Walsh & al. W002* (GENT W002), LN830488*, LN830563*, LN830638*, LN830344*, LN830392* **Cardiandra:** *C. alternifolia* (Siebold) Siebold & Zucc., Japan, 2012, *De Smet & al. YDS 1686* (GENT YDS 1686), LN830445*, LN830520*, LN830595*, LN830301*, LN830369* **C. moellendorffii** (Hance) Migo, China, *BG GU, 2007-1541 PG 11135* (GENT PG 11135), LN830468*, LN830543*, LN830618*, LN830324*, LN830394* **Carpenteria:** *C. californica* Torr., U.S.A., *BG GU, 2003-0248 PG 11191* (GENT PG 11191), LN830476*, LN830551*, LN830626*, LN830332*, LN830399* **Decumaria:** *D. barbara* L., U.S.A., *BG GU, 1996-1362 PG 12385* (GENT PG 12385), HE983586, HE983546, HE983566, HE983426, LN830372* **D. barbara**, U.S.A., *BG GU, 2006-1504 PG 11801* (GENT PG 11801), LN830485*, LN830560*, LN830635*, LN830341*, N.A. **Deinanthe:** *D. bifida* Maxim., Japan, 2012, *De Smet & al. YDS 1692* (GENT YDS 1692), LN830448*, LN830523*, LN830598*, LN830304*, LN830371* **D. caerulea** Stapf, China, *BG GU, 2001-1825 PG 11192* (GENT PG 11192), LN830466*, LN830541*, LN830616*, LN830322*, LN830389* **D. caerulea**, China, *BG GU, 2003-2118 PG 11193* (GENT PG 11193), LN830467*, LN830542*, LN830617*, LN830323*, LN830390* **D. caerulea**, China, *BG GU, 2001-2148 PG 11338* (GENT PG 11338), LN830469*, LN830544*, LN830619*, LN830325*, LN830395* **Dichroa:** *D. febrifuga* Lour., China, *BG GU, 2000-0634 PG 11000* (GENT PG 11000), HE983587*, HE983547*, HE983567*, HE983427*, LN830400* **D. hirsuta** Gagnep., Laos, *BG GU, 2007-1345 PG 11202* (GENT PG 11202), LN830431*, LN830506*, LN830581*, LN830287*, LN830357* **D. hirsuta**, China, *BG GU, 2005-1686 PG 11324* (GENT PG 11324), LN830449*, LN830524*, LN830599*, LN830305*, LN830373* **D. versicolor** D.R.Hunt, Thailand, *BG GU, 2007-1346 PG 12388* (GENT PG 12388), LN830451*, LN830526*, LN830601*, LN830307*, LN830374* **D. yunnanensis** S.M.Hwang, Vietnam, *BG GU, 2007-1366 PG 12338* (GENT PG 12338), LN830452*, LN830527*, LN830602*, LN830308*, LN830375* **Hydrangea:** *H. angustipetala* Hayata, *BG GU, 2006-1310 PG 12379* (GENT PG 12379), HE983588, HE983548, HE983568, HE983428, LN830382* **H. angustipetala** “f. *macrosepala*”, Taiwan, *BG GU, 2006-1313 PG 10797* (GENT PG 10797), LN830432*, LN830507*, LN830582*, LN830288*, LN830358* **H. angustipetala** “f. *macrosepala*”, Taiwan, *BG GU, 2007-1349 PG 11195* (GENT PG 11195), LN830465*, LN830540*, LN830615*, LN830321*, LN830388* **H. anomala** D. Don, Japan, *BG GU, 2007-0627 PG 1101* (GENT PG 1101), LN830426*, LN830501*, LN830576*, LN830282*, LN830355* **H. anomala**, Japan, *BG GU, 2007-0623 PG 11802* (GENT PG 11802), LN830458*, LN830533*, LN830608*, LN830314*, LN830385* **H. anomala**, China, 2011, *De Smet & Rodriguez YDS 1198* (GENT YDS 1198), LN830481*, LN830556*, LN830631*, LN830337*, LN830402* **H. anomala** subsp. *petiolaris* (Siebold & Zucc.) E.M.McClint., Japan, *BG GU, 2007-1359 PG 12383* (GENT PG 12383), HE983589, HE983549, HE983569, HE983429, LN830359* **H. anomala** subsp. *petiolaris*, Japan, *BG GU, 2007-1351 PG 12384* (GENT PG 12384), LN830435*, LN830510*, LN830585*, LN830291*, LN830360* **H. arborescens** L. subsp. *arborescens*, U.S.A., *BG GU, 1983-1495 PG 11806* (GENT PG 11806), LN830454*, LN830529*, LN830604*, LN830310*, N.A. **H. arborescens** subsp. *arborescens*, U.S.A., *BG GU, 1977-2181 PG 10990* (GENT PG 10990), HE983590, HE983550, HE983570, HE983430, N.A. **H. arborescens** subsp. *discolor* Ser., U.S.A., *BG GU, 2001-0237 PG 11002* (GENT PG 11002), LN830484*, LN830559*, LN830634*, LN830340*, LN830406* **H. arborescens** subsp. *radiata* (Walter) E.M.McClintock, U.S.A., *BG GU, 2001-0238 PG 10993* (GENT PG 10993), LN830470*, LN830545*, LN830620*, LN830326*, LN830396* **H. aspera** D. Don, China, 2011, *De Smet & Rodriguez YDS 1142* (GENT YDS 1142), LN830421*, LN830496*, LN830571*, LN830277*, LN830350* **H. chinensis** Maxim., Taiwan, 2011, *Wang YDS 1241* (GENT YDS 1241), LN830427*, LN830502*, LN830577*, LN830283*, LN830356* **H. chinensis** “f. *formosana*”, Taiwan, *BG GU, 2006-1308 PG 11311* (GENT PG 11311), LN830436*, LN830511*, LN830586*, LN830292*, LN830361* **H. chinensis** “f. *formosana*”, Taiwan, *BG GU, 2007-1352 PG 11194* (GENT PG 11194), LN830437*, LN830512*, LN830587*, LN830293*, LN830362* **H. chungii** Rehder, *BG GU, 2006-1306 PG 11334* (GENT PG 11334), LN830473*, LN830548*, LN830623*, LN830329*, LN830398* **H. heteromalla** D. Don, China, 2011, *De Smet & Rodriguez YDS 1096* (GENT YDS 1096), LN830415*, LN830490*, LN830565*, LN830271*, LN830346* **H. heteromalla**, China, 2011, *De Smet & Rodriguez YDS 1098* (GENT YDS 1098), LN830417*, LN830492*, LN830567*, LN830273*, LN830348* **H. heteromalla**, China, 2011, *De Smet & Rodriguez YDS 1157* (GENT YDS 1157), LN830418*, LN830493*, LN830568*, LN830274*, N.A. **H. heteromalla**, China, 2011, *De Smet & Rodriguez YDS 1130* (GENT YDS 1130), LN830420*, LN830495*, LN830570*, LN830276*, LN830349* **H. heteromalla**, China, 2011, *De Smet & Rodriguez YDS 1156* (GENT YDS 1156), LN830422*, LN830497*, LN830572*, LN830278*, LN830351* **H. heteromalla**, China, 2011, *De Smet & Rodriguez YDS 1049* (GENT YDS 1049), LN830423*, LN830498*, LN830573*, LN830279*, LN830352* **H. hirta** (Thunb.) Siebold, Japan, 2012, *De Smet & al. YDS 1610* (GENT YDS 1610), LN830439*, LN830514*, LN830589*, LN830295*, LN830365* **H. indochinensis** Merr., *BG GU, 2007-1368 PG 11203* (GENT PG 11203), LN830462*, LN830537*, LN830612*, LN830318*, LN830384* **H. integrifolia** Hayata, Taiwan, 2011, *De Smet & Rodriguez YDS 1197* (GENT YDS 1197), LN830425*, LN830500*, LN830575*, LN830281*, LN830354* **H. integrifolia**, Taiwan, *BG GU, 2007-1354 PG 12382* (GENT PG 12382), HE983592, HE983552, HE983572, HE983432, LN830387* **H. involucreta** Siebold, Japan, *BG GU, 1998-0525 PG 10995* (GENT PG 10995), HE983593, HE983553, HE983573, HE983433, N.A. **H. involucreta**, Japan, 2012, *De Smet & al. YDS 1672* (GENT YDS 1672), LN830479*, LN830554*, LN830629*, LN830335*, N.A. **H. jelskii** Szyszyl., 2012, *Granados & al. CGM 2012-03* (GENT GCM 2012-03), LN830478*, LN830553*, LN830628*, LN830334*, N.A. **H. lobbiai** Maxim., *BG GU, 2002-2058 PG 11336* (GENT PG 11336), LN830428*, LN830503*, LN830578*, LN830284*, N.A. **H. luteovenosa** Koidz., Japan, *BG GU, 2007-1355 PG 11196* (GENT PG 11196), HE983594, HE983554, HE983574, HE983434, LN830380* **H. macrophylla** (Thunb.) Ser., Japan, 2012, *De Smet & al. YDS 1630* (GENT YDS 1630), LN830471*, LN830546*, LN830621*, LN830327*, LN830397* **H. macrophylla** ‘Ayesha’, Japan, *BG GU, 1900-4502 PG 11804* (GENT PG 11804), HE983595, HE983555, HE983575, HE983435, LN830366* **H. macrophylla** subsp. *serrata* (Thunb.) Makino, Japan, 2012, *De Smet & al. YDS 1653* (GENT YDS 1653), LN830442*, LN830517*, LN830298*, LN830368* **H. paniculata** Siebold, Taiwan, 2011, *De Smet & Rodriguez YDS 1193* (GENT YDS 1193), LN830424*, LN830499*, LN830574*, LN830280*, LN830353* **H. petiolaris** Siebold & Zucc., Japan, 2012, *De Smet & al. YDS 1639* (GENT YDS 1639), LN830441*, LN830516*, LN830591*, LN830297*, LN830367* **H. quercifolia** Bartram, U.S.A., *BG GU, 1997-1102 PG 11807* (GENT PG 11807), HE983597, HE983557, HE983577, HE983437, LN830376* **H. quercifolia** Bartram, U.S.A., *BG GU, 2008-0624 PG 11333* (GENT PG 11333), LN830486*, LN830561*, LN830636*, LN830342*, LN830408* **H. robusta** Hook.f. & Thomson, China, 2011, *De Smet & Rodriguez YDS 1114* (GENT YDS 1114), LN830419*, LN830494*, LN830569*, LN830275*, LN830409* **H. sargentiana** Rehder, China, 2012, *De Smet & Batters YDS 1437* (GENT YDS 1437), LN830483*, LN830558*, LN830633*, LN830339*, LN830405* **H. scandens** (L. F.) Ser., China, *BG GU, 2007-1357 PG 12393* (GENT PG 12393), LN830459*, LN830534*, LN830609*, LN830315*, LN830381* **H. seemannii** L.Riley, Mexico, *BG GU, 2007-0715 PG 10991* (GENT PG 10991), HE983599, HE983559, HE983579, HE983439, N.A. **H. seemannii** × *peruviana*, N.A., *BG GU, 2005-1619 PG 12381* (GENT PG 12381), LN830482*, LN830557*, LN830632*, LN830338*, LN830403* **H. serrata** f. *acuminata* (Siebold & Zucc.) E.H.Wilson, Japan, *BG GU, 2001-1200 PG 11329* (GENT PG 11329), LN830600, HE983600, HE983580, HE983440, LN830377* **H. sikokiana** Maxim., Japan, 2012, *De Smet & al. YDS 1687* (GENT YDS 1687), LN830446*, LN830521*, LN830596*, LN830302*, LN830370* **H. sikokiana**, Japan, *BG GU, 2005-1611 PG 12391* (GENT PG 12391), LN830474*, LN830549*, LN830624*, LN830330*, N.A. **H. strigosa** Rehder, China, *BG GU, 2007-1544 PG s.n.* (GENT PG s.n.), LN830463*, LN830538*, LN830613*, LN830319*, LN830386* **H. stylosa** Hook.f. & Thomson, China, *BG GU, 2006-1309 PG 11199* (GENT PG 11199), LN830472*, LN830547*, LN830622*, LN830328*, LN830412* **Loasa:** *L. tricolor* Lindl., Chile, *BG GU, 2007-0171 PG 10969* (GENT PG 10969), LN830430*, LN830505*, LN830580*, LN830286*, N.A. **Philadelphus:** *P. mexicanus* Schltdl., Mexico, *BG GU, 2004-1782 PG 12390* (GENT PG 12390), LN830489*, LN830564*, LN830639*, LN830345*, LN830393* **P. pekinensis** Rupr., China, *BG GU, 2001-1255 PG 11197* (GENT PG 11197), HE983584, HE983544, HE983564, HE983424, LN830347* **Pileostegia:** *P. viburnoides* Hook.f. & Thomson, Taiwan, *BG GU, 2007-1367 PG 12380* (GENT PG 12380), HE983602, HE983562, HE983582, HE983442, LN830364* **Platyacra:** *P. arguta* Siebold & Zucc., Japan, *BG GU 2010-2507 PG 12389* (GENT PG 12389), HE983601, HE983561, HE983581, HE983441, N.A. **Schizophragma:** *S. hydrangeoides* Siebold & Zucc., *BG GU, 2001-1820 PG 11201* (GENT PG 11201), LN830480*, LN830555*, LN830630*, LN830336*, N.A. **S. integrifolium** var. *saurei* (Hayata) Hayata, *BG GU, 2005-1401 PG 12435* (GENT PG 12435), LN830456*, LN830531*, LN830606*, LN830312*, LN830378* **S. molle** (Rehder) Chun, China, *BG GU, 2004-1309 PG 12394* (GENT PG 11307), HE983603, HE983563, HE983583, HE983443, LN830383* **Xylopodia:** *X. klaprothioides* Weigend, Peru (from cultivation), *Weigend & al. 97/450* (GENT 97/450), LN830475*, LN830550*, LN830625*, LN830331*, N.A.