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A CHLOROPLAST TREE FOR *VIBURNUM* (ADOXACEAE) AND ITS IMPLICATIONS FOR PHYLOGENETIC CLASSIFICATION AND CHARACTER EVOLUTION[1]

WENDY L. CLEMENT[2,7], MÓNICA ARAKAKI[3,5], PATRICK W. SWEENEY[4], ERIKA J. EDWARDS[5], AND MICHAEL J. DONOGHUE[6]

[2]Department of Biology, The College of New Jersey, 2000 Pennington Rd, Ewing, New Jersey 08628 USA; [3]Facultad de Ciencias Biológicas and Museo de Historia Natural, UNMSM, Av. Arenales 1256, Apdo. 14-0434, Lima 14, Perú; [4]Peabody Museum of Natural History, Yale University, P.O. Box 208105, New Haven, Connecticut 06520 USA; [5]Department of Ecology and Evolutionary Biology, Brown University, Box G-W, Providence, Rhode Island 02912 USA; and [6]Department of Ecology and Evolutionary Biology, Yale University, P.O. Box 208106, New Haven, Connecticut 06520 USA

- *Premise of the study:* Despite recent progress, significant uncertainties remain concerning relationships among early-branching lineages within *Viburnum* (Adoxaceae), prohibiting a new classification and hindering studies of character evolution and the increasing use of *Viburnum* in addressing a wide range of ecological and evolutionary questions. We hoped to resolve these issues by sequencing whole plastid genomes for representative species and combining these with molecular data previously obtained from an expanded taxon sample.
- *Methods:* We performed paired-end Illumina sequencing of plastid genomes of 22 *Viburnum* species and combined these data with a 10-gene data set to infer phylogenetic relationships for 113 species. We used the results to devise a comprehensive phylogenetic classification and to analyze the evolution of eight morphological characters that vary among early-branching lineages.
- *Key results:* With greatly increased levels of confidence in most of the early branches, we propose a phylogenetic classification of *Viburnum*, providing formal phylogenetic definitions for 30 clades, including 13 with names recognized under the International Code of Nomenclature for Algae, Fungi, and Plants, eight with previously proposed informal names, and nine newly proposed names for major branches. Our parsimony reconstructions of bud structure, leaf margins, inflorescence form, ruminate endosperm, extrafloral nectaries, glandular trichomes, palisade anatomy, and pollen exine showed varying levels of homoplasy, but collectively provided morphological support for some, though not all, of the major clades.
- *Conclusions:* Our study demonstrates the value of next-generation plastid sequencing, the ease of creating a formal phylogenetic classification, and the utility of such a system in describing patterns of character evolution.

Key words: character evolution; chloroplast DNA; classification; phylogeny; phylogenetic definitions; phylogenetic nomenclature; plastid genome; *Viburnum*.

Over the past decade, much progress has been made in understanding *Viburnum* phylogeny (Donoghue et al., 2004; Winkworth and Donoghue, 2004, 2005; Clement and Donoghue, 2011, 2012). The number of sampled species has increased from 40 to 90, representing all major lineages within the clade. Additionally, sampling has increased from four to 10 gene regions, thus providing better phylogenetic resolution and confidence. These advances have enabled recent studies of leaf form, anatomy, physiology, and phenology in relation to climate and biome shifts (Schmerler et al., 2012; Chatelet et al., 2013; Edwards et al., 2014), defenses against herbivory (Desurmont et al., 2011; Weber et al., 2012), fruit and seed characters (Jacobs et al., 2008), and biogeography in relation to diversification (Winkworth and Donoghue, 2005; Moore and Donoghue, 2007, 2009). While our phylogenetic studies have consistently and strongly supported relationships at midlevels within the phylogeny—corresponding to previously recognized sections and subsections—it has proven difficult to resolve deeper relationships with confidence, as well as very recent divergences within groups of closely related species.

The aims of the present study were (1) to confidently resolve deep relationships within *Viburnum* with the aid of next-generation sequencing of whole plastid genomes, (2) to reflect this new knowledge in a system of phylogenetic nomenclature (without ranks) designed to insure efficient and precise communication, and (3) to illustrate the advantages of this new system in analyzing the evolution of key morphological traits that vary among the early-diverging lineages. This study advances our understanding of *Viburnum* and increases its value for ecologists and evolutionary biologists. More generally, however, we believe it not only provides an example of the great benefits of a committed effort to completely and confidently resolve

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[7]Author for correspondence (e-mail: clementw@tcnj.edu)

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relationships within a clade, but also takes the next major step and translates this knowledge into a system of names that allows us to unambiguously communicate our understanding of evolution.

MATERIALS AND METHODS

Focal clade—*Viburnum* (Adoxaceae, Dipsacales), a clade of ~165 woody angiosperm species, is well known for its diversity in leaf form, bud morphology, growth pattern, flower morphology, fruit color, and endocarp shape. It is distributed widely around the northern hemisphere, in tropical and montane Southeast Asia, and at higher elevations in Mexico, Central America, and the Andes of South America (Venezuela through Bolivia). While temperate eastern Asia and the cloud forests of Latin America are modern centers of *Viburnum* species diversity, Southeast Asia remains the center of phylogenetic diversity (Clement and Donoghue, 2011). Nearly half of all *Viburnum* species have been brought into cultivation (Dirr, 2007).

Taxon sampling for whole plastid sequencing—We sampled 22 species selected to represent all major lineages of *Viburnum* based on prior phylogenetic studies (Table 1; Winkworth and Donoghue, 2005; Clement and Donoghue, 2011). Larger or highly diverse clades, including *Lentago*, *Oreinodontotinus*, and *Solenotinus* were represented by more than one species.

DNA extractions, plastid isolation, and sequencing—For *Viburnum* species collected and dried in silica (Table 1), whole genomic DNA was extracted using a Qiagen DNeasy kit (Qiagen, Valencia, California, USA) following the manufacturer's protocol. For all other species, plastid DNA was isolated from fresh material using the sucrose gradient centrifugation protocol of Jansen et al. (2005). Plastid DNA was amplified using a Qiagen REPLI-g Mini kit (Qiagen, Valencia, California, USA) following Jansen et al. (2007). Amplification products were checked for purity using an EcoR1 digest and visualized on a 1% agarose gel.

Libraries were constructed for 100-bp paired-end sequencing of 400–450-bp fragments on an Illumina platform. First, we fragmented 100 ng of whole genomic DNA or 100 ng of the amplified plastid genome (Table 1) using a NEBNext dsDNA Fragmentase kit (New England Biolabs, Ipswich, Massachusetts, USA). The products were cleaned using a Zymoclean PCR purification kit (Zymo Research, Irvine, California, USA). Selection for 400–450-bp fragments was conducted by first running the cleaned products on a 2% agarose gel prepared with Low Range Ultra Agarose (BioRad, Hercules, California, USA). The 400–450-bp band was manually cut from the gel and cleaned with a Zymoclean Gel DNA Recovery kit (Zymo Research). The cleaned product was enriched using the Illumina-Compatible Nextera DNA Sample Prep Kit, Nextera PCR Enzyme, and Nextera Barcoding Primers (Epicentre Biotechnologies, Madison, Wisconsin, USA). The thermal cycler conditions were as follows: 72°C for 3 min, 95°C for 30 s, and 9 cycles of 95°C for 10 s, 62°C for 30 s, and 72°C for 3 min. Products were cleaned using the Agencourt AMPure XP PCR purification system (Beckman Coulter, Indianapolis, Indiana, USA) and quantified using a Qubit Fluorometer (Invitrogen, Carlsbad, California, USA) and NanoDrop spectrophotometer (Thermo Fisher Scientific, Wilmington, Delaware, USA). Next-generation sequencing was performed at the Genomics Core Facility at Brown University on an Illumina Hi-SEq. 2000 instrument (Illumina Inc., San Diego, California, USA).

Genome assembly and gene region extraction—The sequencing reads with different barcodes were sorted into different assemblies. The quality of the data generated from paired-end sequencing was examined using FastQC (Andrews, 2011). Data were then filtered using the "sanitize" subpipeline of Agalma (Dunn et al., 2013) to remove poor quality sequences and then assembled with the program Yasra 2.2 (Ratan, 2009) using an assembled plastid genome of *Lonicera* as a reference (M. Moore, Oberlin College, unpublished data; individual gene regions extracted from this genome were analyzed and published by Moore et al. [2010]). Within Yasra, the input sequence type was set to "Solexa",

TABLE 1. List of species sampled in whole plastid genome sequencing. Voucher information is provided for each species, along with the clade to which it belongs, and whether plastid isolation or total genomic DNA extractions were used to prepare libraries for next generation sequencing.

Clade	Species	Collector	No.	Collection Locality	DNA
Lobata	*V. acerifolium* L.	M.J. Donoghue	240	Yale Myers Forest, CT, USA	Plastid
	V. amplificatum J. Kern	P.W. Sweeney et al.	2149	Sabah, Malaysia	Total genomic
Euviburnum	*V. carlesii* Hemsl.	W.L. Clement, M.J. Donoghue	245	Marsh Botanical Garden, Yale University, New Haven, CT, USA	Plastid
Lentago	*V. cassinoides* L.	M.J. Donoghue	874-85A	Arnold Arboretum, Boston, MA, USA	Plastid
	V. clemensiae J. Kern	P.W. Sweeney et al.	2142	Sabah, Malaysia	Total genomic
Coriacea	*V. cylindricum* Buch.-Ham. Ex D.Don	M.J. Donoghue, D. Chatelet	WC268	University of Washington Botanical Garden, Seattle, WA, USA	Plastid
Oreinotinus	*V. dentatum* L.	M.J. Donoghue, D. Chatelet	WC244	Marsh Botanical Garden, Yale University, New Haven, CT, USA	Plastid
Succotinus	*V. dilatatum* Thunb.	W.L. Clement, M.J. Donoghue	248	Yale University, New Haven, CT, USA	Plastid
Solenotinus	*V. erubescens* Wall.	M.J. Donoghue, D. Chatelet	WC278	University of Washington Botanical Garden, Seattle, WA, USA	Plastid
Solenotinus	*V. grandiflorum* Wall. ex DC	M.J. Donoghue, D. Chatelet	WC271	University of Washington Botanical Garden, Seattle, WA, USA	Total genomic
Pseudotinus	*V. lantanoides* Miq.	M.J. Donoghue	WC239	Yale Myers Forest, CT, USA	Plastid
Lentago	*V. lentago* L.	W.L. Clement, M.J. Donoghue	242	Marsh Botanical Garden, Yale University, New Haven, CT, USA	Plastid
Lutescentia	*V. lutescens* Bl.	P.W. Sweeney et al.	2077	Ha Giang, Vietnam	Total genomic
Mollotinus	*V. molle* Michx.	M.J. Donoghue	WC238	Arnold Arboretum, Boston, MA, USA	Plastid
Opulus	*V. opulus* L.	W.L. Clement, M.J. Donoghue	250	Yale University, New Haven, CT, USA	Plastid
Lutescentia	*V. plicatum* Thunb.	W.L. Clement, M.J. Donoghue	243	Marsh Botanical Garden, Yale University, New Haven, CT, USA	Plastid
Punctata	*V. punctatum* Buch.-Ham. Ex D.Don	P.W. Sweeney et al.	2097	Kon Tum, Vietnam	Total genomic
Solenotinus	*V. sieboldii* Miq.	W.L. Clement, M.J. Donoghue	249	Marsh Botanical Garden, Yale University, New Haven, CT, USA	Plastid
Urceolata	*V. taiwanianum* Hayata	K-F. Chung et al.	1938	National Taiwan University, Taiwan	Total genomic
Tinus	*V. tinus* L.	M.J. Donoghue, D. Chatelet	WC277	University of Washington Botanical Garden, Seattle, WA, USA	Plastid
Oreinotinus	*V. triphyllum* Benth.	P.W. Sweeney et al.	1783	Loja, Ecuador	Total genomic
Sambucina	*V. vernicosum* Gibbs.	P.W. Sweeney et al.	2123	Sabah, Malaysia	Total genomic

the orientation of the reference sequence was set to "circular", and the expected percentage identity between the reference genome and input data was set to "medium", or about 85% identical. The resulting contigs were concatenated and uploaded to the program Dogma (Wyman et al., 2004) for inspection and to extract coding and noncoding regions that had been successfully assembled. Gene regions were aligned individually with the program Muscle (Edgar, 2004) and manually inspected for alignment errors. Coding regions were translated to check the position of any gaps in the alignment.

***Phylogenetic analyses using plastid genome data*—**All plastid coding regions assembled and aligned were concatenated and analyzed in a single data set as were the plastid noncoding regions. The program jModelTest v 2.1.4 (Guindon and Gascuel, 2003; Darriba et al., 2012) was used to determine the best fitting model of sequence evolution for the plastid coding and noncoding data sets as evaluated by the Akaike information criterion (AIC; Akaike, 1974). Phylogenetic analyses were conducted in both a maximum likelihood (ML) and Bayesian framework. ML analyses were performed with the program Garli v 2.0 (Zwickl, 2006) using the recommended settings. Each analysis was repeated five times to ensure that likelihood scores were similar among runs. Additionally, ML bootstrap analyses with 500 replicates were performed on each data set. Bayesian analyses were conducted using MrBayes v 3.2.1 (Huelsenbeck and Ronquist, 2001; Ronquist et al., 2012). Each analysis was run for 30 million generations with six chains sampling the posterior every 1000 generations. Convergence of the analysis and burn-in (no less than 10%) were determined visually by inspecting plots of all parameters in the program Tracer v 1.5 (Rambaut and Drummond, 2009). The burn-in was removed prior to summarizing model parameters and sampling trees from the posterior distribution.

The plastid coding and noncoding data were concatenated and analyzed under two partitioning schemes. First, the data were analyzed under a single model. Second, we used a 2-partition scheme separating coding and noncoding gene regions. Each partition was assigned its own model and parameters were estimated for each partition separately. The ML and Bayesian analyses were conducted as described above except we increased the generations to 40 million. Additionally, in the 2-partitioned Bayesian analysis, all parameters were unlinked.

***Phylogenetic analysis of combined data*—**We assembled a data set for 113 species by combining 10-gene data sets generated previously by Clement and Donoghue (2011) and Chatelet et al. (2013). Since the present analysis represented a new combination of taxa, we first conducted ML and Bayesian phylogenetic analyses as described above. Bayesian analyses were run with six chains for 25 million generations. The same partitioning scheme as Clement and Donoghue (2011) was implemented for both ML and Bayesian analyses and included a partition of plastid coding regions (*matK*, *ndhF*, and *rbcL*), a partition of plastid noncoding regions (*petB-petD*, *rpl32-trnL*^{UAG}, *trnC-ycf6*, *trnH-psbA*, *trnK*, and *trnS-trnG*), and a partition for the internal transcribed spacer region (ITS). Conflicts between the ITS and plastid phylogenies have been detected in the *Pseudotinus* and *Lentago* clades (Winkworth and Donoghue, 2004, 2005; Clement and Donoghue, 2011). However, these conflicts do not appear to affect our ability to infer relationships among the major clades.

The plastid genome data were then combined with the 113-taxon, 10-gene data set. As all 22 species with sequenced whole plastid genomes were also included in our 10-gene data set, the data generated from the plastid genomes were concatenated with the corresponding taxa in the 113-taxon, 10-gene data set. Gene regions in common (namely *matK*, *ndhF*, *rbcL*, *trn*K, and *trnS-trnG*) were removed from the plastid genomic data prior to analysis to avoid duplication. The ML and Bayesian analyses were conducted as previously described except with four chains and 40 million generations. Also, three different partitioning schemes were implemented. First, we used a 5-partition analysis following the 3-partition scheme of Clement and Donoghue (2011) with two additional partitions, one for plastid genome coding data and another for plastid genome noncoding regions generated for the 22 species whose plastid genomes we sequenced. Second, a 3-partition analysis was conducted with one partition for all plastid coding regions (from both Sanger and plastid genome sequencing), a second for all plastid noncoding regions (from both Sanger and plastid genome sequencing), and a third for ITS. The third partitioning scheme was a 2-partition analysis with one partition including all plastid data and the second partition including ITS.

***Rooting*—**Recent publications on *Viburnum* phylogeny (Clement and Donoghue, 2011, 2012) have used *V. clemensiae* to root the tree. Support for the position of *V. clemensiae* as sister to all other *Viburnum* species was first recovered analyzing *trnH-psbA* and *trnK* sequence data (Donoghue et al., 2004; Winkworth and Donoghue, 2005), using *Sambucus canadensis* L. and *S. racemosa* L. as the outgroup. Clement and Donoghue (2011) recovered support for this position of *V. clemensiae* with seven additional chloroplast gene regions. Phylogenetic analyses using ITS or the nuclear granule bound starch synthase gene (GBSSI) have not confidently placed *V. clemensiae*, but have not conflicted with the placement of *V. clemensiae* supported by chloroplast data (Winkworth and Donoghue, 2004; Moore and Donoghue, 2007, 2009).

As the present study represents a significant increase in both taxon and gene sampling, we further explored the rooting using three species of *Sambucus*: *S. canadensis*, *S. peruviana* Kunth, and *S. racemosa*. Focusing on the nine previously studied chloroplast regions, we found increased support for the placement of *V. clemensiae* as sister to all other *Viburnum* species (99% bootstrap support from ML analysis conducted in RAxML [Stamatakis, 2014] with 500 bootstrap replicates). Although we attempted to obtain a whole plastid genome sequence from *S. canadensis*, we encountered sufficient difficulties in assembly and alignment that we have not included additional plastid markers for outgroups. This issue will be explored in greater depth when we succeed in assembling whole plastid genomes from a number of outgroup species and obtain additional nuclear data beyond the ITS sequences included here. As in prior studies, our expanded ITS analyses (113 *Viburnum* species plus several *Sambucus* species) fail to confidently resolve the position of the root of *Viburnum*. For the time being, based on the strong support provided by the nine plastid genes, we have rooted our *Viburnum* trees along the branch leading to *V. clemensiae*.

***Character evolution*—**We selected eight discrete morphological and anatomical characters for study in a phylogenetic framework. Each of these has appeared to mark major clades deep within the tree. Four have traditionally been used to identify major groups and appear among the primary couplets of dichotomous keys to *Viburnum* (e.g., Kern, 1951; Hara, 1983; Yang and Malecot, 2011): (1) bud morphology—naked or with bud scales; (2) leaf margins—entire or variously toothed; (3) inflorescence architecture—umbel-like or panicle-like; (4) ruminate endosperm—absent or present. Four other, less obvious, characters have been discovered in more recent surveys to mark major clades: (1) extrafloral nectaries—absent, marginal, laminar, or petiolar (Weber et al., 2012); (2) glandular trichomes—elongate, capitate, or peltate (present study); (3) palisade anatomy—one layer of H-shaped cells (H-1), two layers of H-shaped cells (H-2), one layer of I-shaped cells (I-1), or two layers of I-shaped cells (I-2) (Chatelet et al., 2013); and (4) pollen exine muri—smooth or scabrate (Donoghue, 1985). We excluded from consideration a number of conspicuous characters on the grounds that they vary too much within major clades and species complexes (e.g., evergreen vs. deciduous leaves), are consistent but present in just a few species (e.g., trilobed leaves), or are highly scattered in occurrence (e.g., pit domatia). Other traits have been (e.g., endocarp shape [Jacobs et al., 2008]) or are being analyzed in detailed elsewhere (e.g., corolla form, fruit color).

The eight characters under consideration, which are described in greater detail in the Results and Discussion, were scored for the 22 species included in the plastid genome study, but accounting (using polymorphic coding where necessary) for known variation present across the major clades that these species represent. For this purpose, we referred to prior literature (Kern, 1951; Hara, 1983; Donoghue, 1985; Jacobs et al., 2008; Yang and Malecot, 2011; Weber et al., 2012; Chatelet et al., 2013) and relied on our own extensive field, laboratory, and herbarium observations. Pollen grains and leaf segments were prepared for scanning electron microscopy (SEM) by taking material directly from herbarium specimens, mounting them on a carbon tab stub, and sputter coating them with platinum for 45 s at 40 mA. SEM images were taken using a Phillips XL-30 environmental scanning electron microscope (ESEM) in the Yale Department of Geology & Geophysics. All of the SEM images were minimally edited in Adobe Photoshop CS5.1 (Adobe, San Jose, California, USA) by applying "auto-levels". In the case of the whole pollen grain, the background was removed by using the magnetic lasso (width: 10 px, contrast: 10%, frequency: 57) to select the edge of the pollen grain and using the paint bucket to blacken the image outside of the selected area. Field images of leaves illustrating extrafloral nectaries were manipulated by blackening the background to black using the paintbrush feature in Adobe Photoshop CS5.1.

Parsimony and maximum likelihood ancestral state reconstructions were performed in the program Mesquite v 2.75 (Maddison and Maddison, 2011) using the combined coding and noncoding plastid genome phylogeny. ML reconstructions were calculated under a Markov *k*-state 1-parameter model (Mk1) that assumes all transitions among discrete character states are equal (Lewis, 2001; Maddison and Maddison, 2011). ML reconstructions were carried out using the molecular branch lengths and also with all branch lengths set to 1, and

considering all alternative scorings of polymorphic terminal taxa. A more complete statistical analysis, to be conducted in the context of a nearly completely sampled and dated phylogeny, awaits the completion of a comprehensive morphological matrix for *Viburnum*.

RESULTS AND DISCUSSION

Plastid genomes and phylogenetic analysis—Information concerning the raw Illumina sequence data collected (e.g., number of reads, reads used in assembly) is available in Appendix S1 (see Supplemental Data with online version of this article). Coverage of *Viburnum* plastids ranged from 21× to 3903×. We recovered 73 coding regions (52 758 bp) and 51 noncoding regions (16 819 bp). Although we recovered fewer gene regions than are actually present in the chloroplast genome, we limited our analysis to those gene regions we could reliably assemble and align. Our reference-based assemblies showed greater coverage across regions of the plastid that correspond to coding genes as compared with intergenic spacer regions. To this end, we have a much more complete sample of coding as compared with noncoding regions of the plastid, thus explaining why we did not recover some gene regions we have used in prior phylogenetic studies of *Viburnum* (including *trnH-psbA*, *rpl32-trnL*, *petB-petD*, and *trnC-ycf6*). The matrix of gene regions sampled from the plastid sequencing was nearly complete, with a few exceptions—*V. dentatum* and *V. tinus* were missing from *trnL*^{UAG}-*ccsA*, and *V. vernicosum* was missing from *ndhA*, *ndhE*, *ndhG*, *ndhH*, *ndhI*, *psaC*, and *rps15*. A list of gene regions and GenBank accession numbers is provided in Appendix 1, and complete data matrices are available in the TreeBASE database (http://purl.org/phylo/treebase/phylows/study/TB2:S15758) and the Dryad Digital Repository (doi:10.5061/dryad.hh12b).

A TVM+I+G model of sequence evolution was selected for the coding regions combined and for the noncoding regions combined. Both data sets generally supported the same relationships, and we found no instances of well-supported conflicts between the trees inferred from the coding and noncoding regions (Appendices S2, S3, see online Supplemental Data). Overall, the phylogeny based on the noncoding data were less well resolved and exhibited lower clade support values as compared to the coding data.

Given the lack of conflict between the two data sets, we concatenated the data and analyzed a combined data set that included 124 gene regions and 69 577 bp. A 2-partition scheme (one partition for coding data and a second for noncoding data) resulted in higher likelihood scores for both ML (2-partition: −lnL = 117 274.4894; 1-partition: –lnL = 117 624.473) and Bayesian analyses (2-partition: −lnL = 119 110.64; 1-partition: −lnL = 119 458.33). The Bayesian majority rule consensus tree for the entire 22-species plastid data set is shown in Fig. 1. This tree is consistent with, but greatly increases confidence over prior phylogenetic analyses of *Viburnum* (Clement and Donoghue, 2011, 2012; Chatelet et al., 2013).

Phylogenetic analysis of the 113-species data set derived by combining the 10-gene data sets of Clement and Donoghue (2011) and Chatelet et al. (2013) produced a tree that was congruent with previously published phylogenies (online Appendix S4; see Appendix 2 for full list of gene regions and GenBank accession numbers). Concatenation of all of the data—our new plastid data for 22 species plus the data for 113 species—resulted in a data set with 129 gene regions and 71 935 bp. This data set yielded the tree shown in Fig. 2. We found that a 2-partition scheme identified a tree with the best likelihood score for both ML and Bayesian analyses (ML: −lnL = 135 511.9665 for 5-partition, −lnL = 135 484.8781 for 3-partition, and −lnL = 133 107.5295 for 2-partition; Bayes: 5-partition, analysis did not converge, −lnL = 134 583.13 for 3-partition, and −lnL = 133 403.74 for 2-partition). There were no significant differences between the topologies that resulted from the 2- and 3-partition analyses. All data sets and published trees from this study are available in TreeBASE (S15758) and Dryad (doi:10.5061/dryad.hh12b).

Phylogenetic implications from plastid phylogeny—The tree in Fig. 1 is labeled with the names of clades that are currently in use and for continuity with past studies these names will be used to orient the discussion of our phylogenetic results. Later in the paper, following our proposal of a new classification system, we will switch to the use of the new names to illustrate how these aid the discussion of character evolution. As noted already, the *Viburnum* tree is rooted along the long *V. clemensiae* branch based on previous analyses (Winkworth and Donoghue, 2005; Moore and Donoghue, 2007, 2009) and on our expanded studies using *Sambucus* as an outgroup. As discussed later, this first deep split within *Viburnum* is consistent with the many morphological differences between *V. clemensiae* and all of the other species.

Relationships remain poorly resolved at the base of the main *Viburnum* clade (excluding *V. clemensiae*) and are best represented by a basal trichotomy that includes the *Valvatotinus* clade, the *Pseudotinus* clade, and a clade containing all remaining *Viburnum* (Fig. 2). This uncertainty is largely due to the unstable position of the *Pseudotinus* clade (represented by *V. lantanoides* Miq.). In some analyses, it appears as sister to the *Valvatotinus* clade, as shown in Figs. 1 and 2; in other analyses (e.g., Winkworth and Donoghue, 2004, 2005), it is sister to the clade with all remaining *Viburnum* (Fig. 2).

Within the well-supported *Valvatotinus* clade, this analysis confirms the monophyly of the *Lentago* clade and also the connection between the tropical Southeast Asian *V. punctatum* Buch.-Ham ex D. Don (representing *Punctata*) and the temperate eastern Asian *Lantana* clade. Two sister clades are well supported within the clade that contains all remaining *Viburnum* species. The first is an entirely Asian clade containing *V. taiwanianum* (representing *Urceolata*) of Taiwan and Japan, the rare *V. amplificatum* J. Kern of northern Borneo, the *Lutescentia* clade containing the tropical *V. lutescens* Bl. and its relatives plus the temperate *V. plicatum* Thunb., and the *Solenotinus* radiation (represented here by *V. grandiflorum* Wall. ex DC, *V. erubescens* Wall., and *V. sieboldii* Miq.). The second is *Imbricotinus* (Winkworth and Donoghue, 2005), which contains the informally named clades *Tinus*, *Succodontotinus*, *Lobata*, *Coriacea*, *Sambucina*, *Opulus*, *Mollodontotinus*, and *Oreinodontotinus.*

One important difference between this result and that of Clement and Donoghue (2011) concerns the placement of *V. amplificatum*. Whereas this species was placed previously as sister to the *Solenotinus* clade (consistent with the original interpretation based on endocarp shape of Kern [1951]), in the present analysis it is placed with confidence even deeper in the tree, as sister to a larger clade including both *Lutescentia* and *Solenotinus*. Within *Solenotinus*, we note confirmation of the placement by Chatelet et al. (2013) of the Himalayan *V. grandiflorum* as sister to the remainder of the clade.

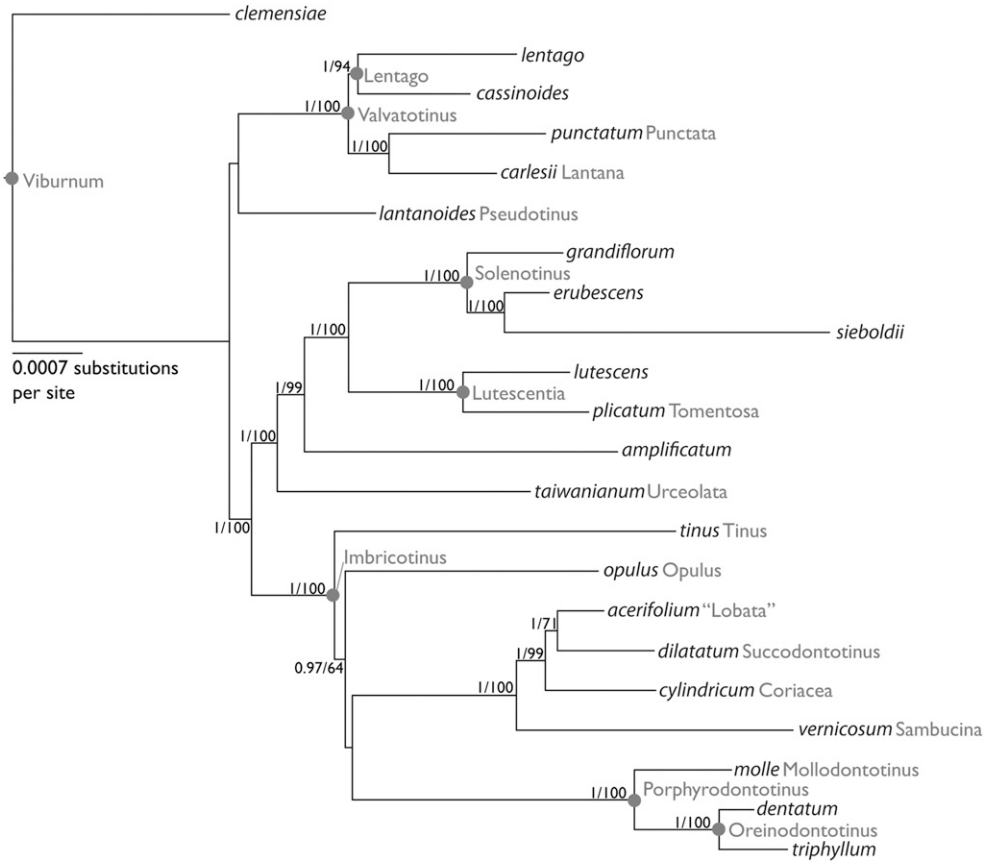


Fig. 1. Bayesian majority-rule consensus tree of plastid genome data analyzed under a 2-partition model. Informal clade names used by Winkworth and Donoghue (2005) and Clement and Donoghue (2011, 2012) are shown in gray. Posterior probabilities (pp) greater than or equal to 0.95 and maximum likelihood (ML) bootstrap values greater than 60% are indicated above or below the branches (pp/ML). Names referring to internal nodes on the phylogeny have been identified with a gray dot.

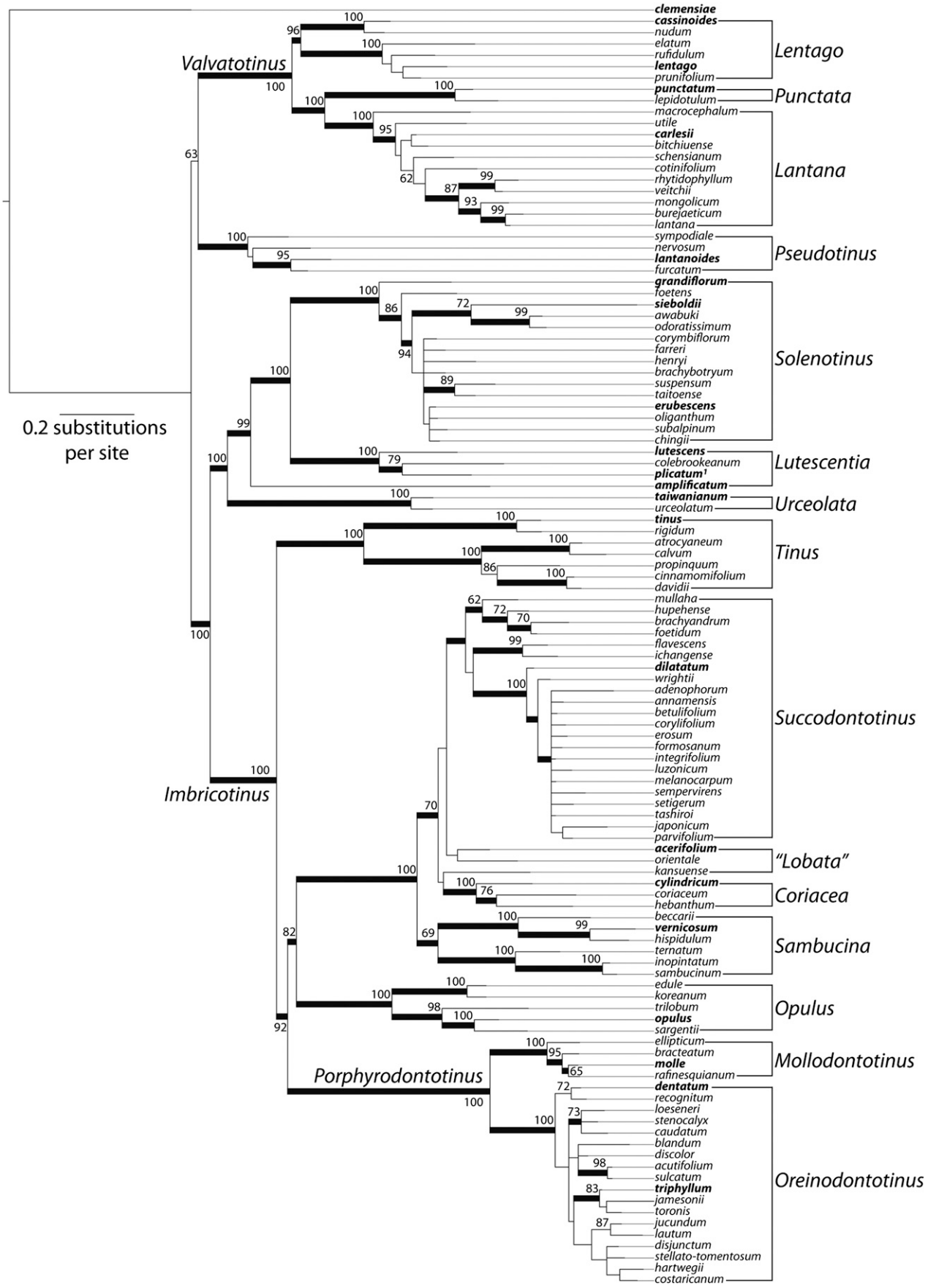
Within what Winkworth and Donoghue (2005) referred to as the *Imbricotinus* clade, there is now better support for the placement of the *Tinus* clade as sister to the rest of the species. The position of the *Opulus* clade is less certain compared with previous analyses (Clement and Donoghue, 2011, 2012). As shown in Fig. 1, it may be sister to a clade containing the New World *Porphyrodontotinus* clade plus the unnamed, almost entirely Old World clade (with the exception of *V. acerifolium* L.) containing the *Sambucina*, *Coriacea*, *Succodontotinus*, and *Lobata* clades. However, there is little support for this position, and *Opulus* could be sister to the Old World clade or to *Porphyrodontotinus* (see Fig. 1).

Within *Porphyrodontotinus*, our results confirm the close relationship between *V. dentatum* L. of eastern North America and the Latin American radiation represented here by *V. triphyllum* Benth. Within the Old World clade, the tropical *Sambucina* and *Coriacea* clades are successively related to the large, mainly temperate eastern Asian *Succodontotinus* clade plus the small circum-northern hemisphere *Lobata* group, represented here by the North American *V. acerifolium*.

In summary, all relationships within our 22-species plastid tree are confidently resolved with the exception of the positions of *V. lantanoides* of the *Pseudotinus* clade and *V. opulus* L. of the *Opulus* clade. In these two cases, only a few alternative placements remain viable.

Phylogenetic implications from the combined data set— Focusing only on confidently resolved relationships among the major clades, the tree in Fig. 2 is entirely consistent with the 22-species plastid tree. When the tree is rooted along the *V. clemensiae* branch, the same three major clades (*Valvatotinus*, *Pseudotinus*, and a clade with all remaining *Viburnum*) are evident at the base of the main *Viburnum* clade. Because the placement of the *Pseudotinus* clade remains uncertain (compare to Fig. 1), these relationships are best represented by an unresolved trichotomy. We note that we also recovered the conflicts previously reported among species within *Pseudotinus,* namely that some plastid gene regions support the sister relationship between *V. furcatum* and *V. nervosum* (Donoghue et al., 2004; Clement and Donoghue, 2011), while nuclear data and other plastid gene regions support the sister relationship of *V. furcatum* and *V. lantanoides* to the exclusion of *V. nervosum* (Winkworth and Donoghue, 2004, 2005). This conflict could potentially reflect homoploid hybrid speciation within this group (Winkworth and Donoghue, 2005).

Within *Valvatotinus*, *Lentago* continues to form a well-supported clade, within which there is a deep split between *V. nudum* L. plus *V. cassinoides* L. and the remainder of the species. Support for relationships among species of *Lentago* decreased in the combined analysis as compared with the analysis of the 10 genes (Appendix S4). This could reflect conflict between


0.2 substitutions per site
Valvatotinus
Imbricotinus
Porphyrodontotinus
clemensiae
cassinoides
nudum
elatum
rufidulum
lentago
prunifolium
Lentago
punctatum
lepidotulum
Punctata
macrocephalum
utile
carlesii
bitchiuense
schensianum
cotinifolium
rhytidophyllum
veitchii
mongolicum
burejaeticum
lantana
Lantana
sympodiale
nervosum
lantanoides
furcatum
Pseudotinus
grandiflorum
foetens
sieboldii
awabuki
odoratissimum
corymbiflorum
farreri
henryi
brachybotryum
suspensum
taitoense
erubescens
oliganthum
subalpinum
chingii
Solenotinus
lutescens
colebrookeanum
plicatum¹
amplificatum
Lutescentia
taiwanianum
urceolatum
Urceolata
tinus
rigidum
atrocyaneum
calvum
propinquum
cinnamomifolium
davidii
Tinus
mullaha
hupehense
brachyandrum
foetidum
flavescens
ichangense
dilatatum
wrightii
adenophorum
annamensis
betulifolium
corylifolium
erosum
formosanum
integrifolium
luzonicum
melanocarpum
sempervirens
setigerum
tashiroi
japonicum
parvifolium
Succodontotinus
acerifolium
orientale
kansuense
"Lobata"
cylindricum
coriaceum
hebanthum
Coriacea
beccarii
vernicosum
hispidulum
ternatum
inopintatum
sambucinum
Sambucina
edule
koreanum
trilobum
opulus
sargentii
Opulus
ellipticum
bracteatum
molle
rafinesquianum
Mollodontotinus
dentatum
recognitum
loeseneri
stenocalyx
caudatum
blandum
discolor
acutifolium
sulcatum
triphyllum
jamesonii
toronis
jucundum
lautum
disjunctum
stellato-tomentosum
hartwegii
costaricanum
Oreinodontotinus

chloroplast and nuclear ribosomal phylogenies that supports the hypothesized hybrid origin of *V. prunifolium* (Winkworth and Donoghue, 2004, 2005). *Punctata* (including *V. punctatum* and *V. lepidotulum* Merr. & Chun) is strongly united with *Lantana*. Relationships at the base of *Lantana* remain uncertain, but several strongly supported subclades are evident for the first time within the core clade (*V. veitchi* C.H. Wright + *V. rhytidophyllum* Hemsl.; *V. lantana* L. + *V. burejaeticum* Regel & Herd.).

We recover confident support for the sister group relationship between *Imbricotinus* (sensu Winkworth and Donoghue, 2005) and the clade including *Urceolata*, *Lutescentia*, and *Solenotinus*. In agreement with the 22-species tree, *V. amplificatum* is sister to the large clade including *Lutescentia* and *Solenotinus*. However, we note that the gene tree based only on *trnS-trnG* places *V. amplificatum* as sister to all of *Viburnum* aside from *V. clemensiae*, suggesting a much deeper divergence for this poorly known species.

Within *Solenotinus*, *V. grandiflorum* retains its position as sister to the rest, and we note a strongly supported clade including *V. sieboldii* + (*V. odoratissimum* Ker Gawl. + *V. awabuki* K. Koch). Among the individual gene phylogenies, *rbcL* is alone in directly uniting the morphologically similar *V. grandiflorum* and *V. foetens* Decne. and placing them as sister to the remainder of *Solenotinus*. Gene trees of *trnC-ycf6*, *trnK*, and *trnS-trnG* conflict with this and are responsible for placing *V. grandiflorum* alone as sister to all other *Solenotinus*. *Viburnum grandiflorum* and *V. foetens* are diploids ($2n = 16$), while all other *Solenotinus* species studied (except *V. farreri* Stearn, also a diploid) are tetraploids (with 32 chromosomes) on what we now infer to be the evolutionarily derived base number of $x = 8$ in *Solenotinus* (Egolf, 1962).

The combined analysis also recovers the *Tinus* clade as sister to the rest of *Imbricotinus*. Within *Tinus*, we note a deep split between the European *V. tinus* L. plus *V. rigidum* Vent. and the remainder of the species, which are Asian. The *Opulus* clade appears in Fig. 2 as sister to the clade including *Sambucina*, *Coriacea*, *Lobata*, and *Succodontotinus*, a result most strongly supported (ML bootstrap = 99%, posterior probability [pp] = 1) in the 10-gene analysis (online Appendix S4) as compared with the combined analysis (ML bootstrap = 82%, pp = 1; Fig. 2). Within *Opulus*, *V. edule* Raf. and *V. koreanum* Nakai are sister to the *V. opulus* clade, which is marked by inflorescences with sterile marginal flowers.

Within *Porphyrodontotinus*, we find a deep split between the *Mollodontotinus* and *Oreinodontotinus* clades. *Viburnum dentatum* and *V. recognitum* Fernald appear as sister to the Latin American species, but this is weakly supported, and it remains possible that *V. dentatum* and its several segregates are nested within the Latin American clade. Within the Latin American clade, it is noteworthy that the South American species appear to form a clade (ML bootstrap = 94%, pp = 1 in the 10-gene analysis [Appendix S4]; ML bootstrap = 83%, pp = 1 in the combined data [Fig. 2]).

Within the remaining largely Old World clade, the *Sambucina* clade is sister to the rest, although ML clade support for *Sambucina* decreases in our combined analysis while posterior probabilities remain high (Appendix S4). Within *Sambucina*, we note that *V. beccarii* Gamble of mainland Malaysia, which was placed by Kern (1951) into subsection *Coriacea*, is instead strongly united with *V. hispidulum* J. Kern and *V. vernicosum* Gibbs from Borneo.

A clade containing *Succodontotinus*, *Lobata*, and *Coriacea* is supported by posterior probabilities in the 10-gene and combined analyses (Fig. 2; Appendix S4), although the ML bootstrap values decrease from 84% in the combined data analysis to 70% in the 10-gene analysis (Fig. 2; Appendix S4). It is noteworthy that the three species (*V. acerifolium*, *V. orientale* Pall., and *V. kansuense* Batalin) assigned previously to *Lobata*, based on their trilobed leaves, do not form a clade in Fig. 2 (or in Appendix S4). However, based on current evidence, it is still possible that these are united as there is no clade support that precludes the formation of a clade containing these three species. The position of the Chinese *V. kansuense* is especially labile, while the North American *V. acerifolium* appears to be related to the morphologically similar *V. orientale* from the Caucasus region of Georgia. Relationships within the large eastern Asian *Succodontotinus* clade remain especially poorly resolved, and it is now clear that progress in sorting out these relationships will require a different approach.

***Phylogenetic classification*—**Based on the strongly supported and congruent phylogenetic results reported here (especially with respect to most of the deepest relationships), and on the increasing need to communicate concisely and unambiguously about *Viburnum* phylogeny in connection with a wide variety of evolutionary and ecological analyses, we take this opportunity to provide a new phylogenetic classification (cf. Cantino et al., 2007). Such a classification is appropriate now, as our sampling has improved greatly (113 of an estimated 164 species), and we are confident that all remaining species can be placed into the clades identified here, which insures stability with respect to clade membership. It should also be evident from the sometimes cumbersome discussion above that names are unavailable for a number of major clades that we already need to discuss.

Figure 3 and Table 2 summarize our new classification system, highlighting 30 clades that are now provided with formal phylogenetic definitions. The two species in Fig. 3, *V. clemensiae* and *V. amplificatum*, are not given phylogenetic definitions as they are single species rather than clades. Additionally, the monophyly of *Lobata* and of *V. lutescens* and its relatives remains too uncertain to warrant naming at this time. The 13 names shown in black are those that have long been recognized under the International Code of Nomenclature for Algae, Fungi, and Plants (ICN). Here we convert these ICN names from preexisting rank-based names to phylogenetic names by providing formal phylogenetic definitions (Table 2). Hara (1983) summarized

←

Fig. 2. Bayesian majority-rule consensus tree of 113 species of *Viburnum*. Data generated from the whole plastid sequencing were combined with data from 10 gene regions previously sampled for *Viburnum* (Clement and Donoghue, 2011; Chatelet et al., 2013). Informal clade names used by Winkworth and Donoghue (2005) and Clement and Donoghue (2011, 2012) are indicated to the right or along a branch leading to an internal node in the phylogeny. Names in bold indicate species for which the plastid genome was sequenced. ML bootstrap values greater than 60% are indicated above or below the branches; thickened branches indicate posterior probabilities greater than 0.95. [1]*V. plicatum* belongs to the formally named clade, *Tomentosa*, which also includes *V. hanceanum* (not included here).

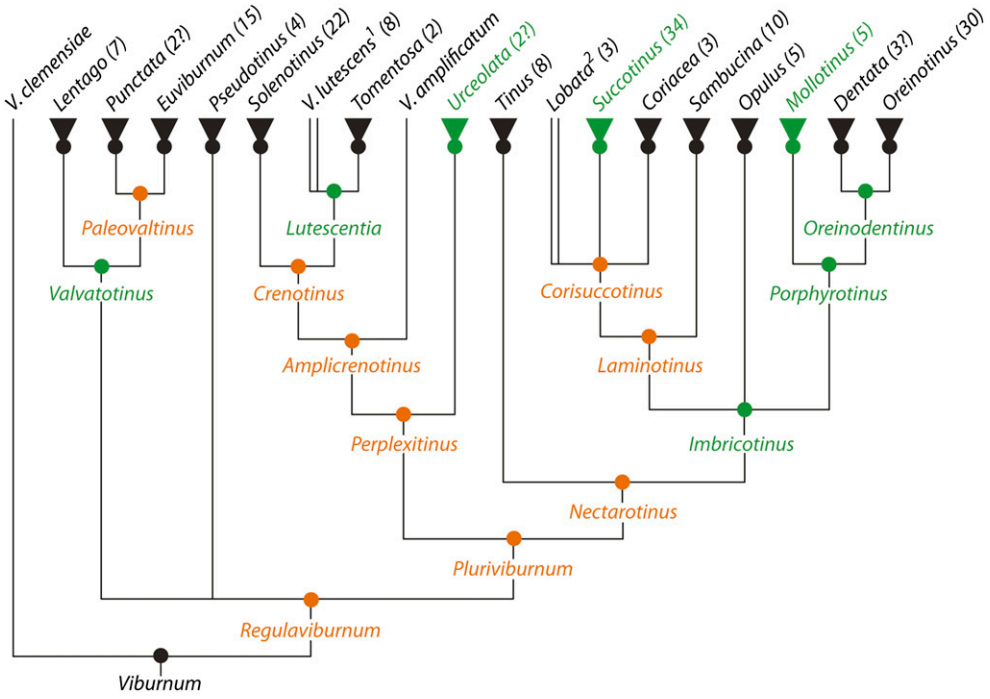


Fig. 3. Proposed phylogenetic classification for *Viburnum* (see also Table 2). Named clades have been identified on the phylogeny with colored dots indicating origin of proposed phylogenetic name as follows. Names and clades marked in black represent previously published names under the ICN that are here converted to phylogenetic names (Table 2). Those in green represent names proposed by Winkworth and Donoghue (2005) and Clement and Donoghue (2011). Several of these names have been shortened by removing the "donto" portion of the name (e.g., *Mollodontotinus* is now *Mollotinus*). Additionally, *Imbricotinus* now refers to a clade that does not include *Tinus*, which differs from the membership of *Imbricotinus* indicated in Fig. 2. Clade names in orange represent names new to the classification of *Viburnum*. The number of species belonging to each terminal clade is given in parentheses. Species counts followed by question marks indicate clades that could, upon further taxonomic investigation, be reduced to a single species, therefore rendering the proposed name unnecessary. [1]*V. amplifolium*, *V. colebrookeanum*, *V. garrettii*, *V. junghunii*, *V. laterale*, and *V. pyramidatum*, in addition to *V. lutescens*, are members of *Lutescentia*. It is possible that some of these species are more closely related to *Tomentosa* (which includes *V. plicatum* and *V. hanceanum*) than to *V. lutescens*. [2]*V. acerifolium*, *V. kansuense*, and *V. orientale* have been placed in the informally named clade *Lobata* (e.g., Winkworth and Donoghue, 2005); however, these do not form a clade in Fig. 2, and *Lobata* is not provided with a phylogenetic definition in Table 2.

the nomenclatural history for each of these names, and relevant authors and publication dates are cited in Table 2.

Winkworth and Donoghue (2005) introduced eight informal clade names, and Clement and Donoghue (2011, 2012) added two more (*Lutescentia* and *Urceolata*). Eight of these 10 are represented in green in Fig. 3; the name *Erythrodontotinus* from Winkworth and Donoghue (2005) is not defined here because there is now little support for this clade, and *Lantana* will be discussed later. These names were never validly published under the ICN and are therefore not considered to be converted names. They were also not given phylogenetic definitions. Because these were never formally published, in several cases, we are taking this opportunity to modify the form of the names, mainly to make them shorter and easier to pronounce by removing the "donto" portion from the name. Specifically, *Succo**donto**tinus* is now *Succotinus*, *Mollo**donto**tinus* is now *Mollotinus*, and *Porphyro**donto**tinus* is now *Porphyrotinus*. However, dropping the "donto" from *Oreino**donto**tinus* would create a synonym with the legitimately published *Oreinotinus*. In this case, we have modified *Oreino**donto**tinus* to *Oreinodentinus*, which combines the prefixes of the names of the two included clades. We note that Winkworth and Donoghue (2005) used the name *Lantana* to refer to the clade that had previously been named section *Viburnum* so as to avoid the confusion of having two clades named *Viburnum*. However, in view of the widespread use of the name *Lantana* for a clade within Verbenaceae, we abandon this name here and instead adopt the name *Euviburnum* for this clade. *Euviburnum* is ideal in this context because Oersted (1861) proposed this name in 1861 for a subgenus corresponding to this clade.

One of Winkworth and Donoghue's informal names—*Imbricotinus*—requires additional discussion. Here we have retained the name, but have changed the clade to which it refers. Winkworth and Donoghue (2005) intended to include the *Tinus* clade within *Imbricotinus*, but we have excluded *Tinus* here, and instead have applied the name *Imbricotinus* to a less inclusive clade. There are two reasons for this change. First, the name was originally intended to refer to the presence of imbricate bud scales, but we now appreciate that such scales are often not present in *Tinus*, which then technically have naked buds (see *Character evolution* below). Second, the clade formerly referred to as *Imbricotinus* is now marked by an unambiguous apomorphy—the presence of extrafloral nectaries on the leaves—and we want to reflect this in the name of the clade. We therefore propose the new name *Nectarotinus* for the former *Imbricotinus* clade (see below).

The nine names shown in orange are proposed here for the first time and are necessary to refer in full to the deepest clades within *Viburnum*—those inferred with confidence in the present

TABLE 2. *Viburnum* classification and phylogenetic nomenclature. Proposed phylogenetic names are presented along with the original author and publication date of the name. Two types of phylogenetic definitions (Def Type) are implemented and are as follows: min: minimum-clade definitions, taking the form: "the smallest clade containing specifier A + specifier B;" and max: maximum-crown-clade definitions, taking the form: "the largest crown clade containing specifier A but not specifier B." Colors correspond to Fig. 3: names in black represent previously published names, names in green represent names first proposed by Winkworth and Donoghue (2005) or Clement and Donoghue (2011, 2012), and names in orange are new to *Viburnum* classification.

Clade name	Author	Pub. Date	Def Type	Specifiers for Phylogenetic Definition[1]
Viburnum	Linnaeus	1753	min	*clemensiae* + *triphyllum*
V. clemensiae	Kern	1951	—	—
Regulaviburnum	Donoghue & Clement	2014	min	*lentago* + *lantanoides* + *triphyllum*
Valvatotinus	Winkworth & Donoghue	2005	max	*lentago*, not *lantanoides* or *triphyllum*
Lentago	DeCandolle	1830	min	*nudum*[2] + *lentago*
Paleovaltinus	Donoghue & Clement	2014	min	*punctatum* + *carlesii*
Punctata	Kern	1951	min	*punctatum* + *lepidotulum*
Euviburnum	Oersted	1861	max	*carlesii*, not *punctatum* or *nudum*
Pseudotinus	C.B. Clarke	1880	max	*lantanoides*, not *lentago* or *triphyllum*
Pluriviburnum	Donoghue & Clement	2014	max	*triphyllum*, not *lentago* or *lantanoides*
Perplexitinus	Donoghue & Clement	2014	min	*urceolatum*[3] + *sieboldii*
Urceolata	Winkworth & Donoghue	2005	min	*urceolatum* + *taiwanianum*
Amplicrenotinus	Donoghue & Clement	2014	max	*sieboldii*, not *urceolatum*[3]
V. amplificatum	Kern	1951	—	—
Crenotinus	Donoghue & Clement	2014	min	*lutescens* + *sieboldii*
Solenotinus	DeCandolle	1830	max	*sieboldii*, not *lutescens*
Lutescentia	Clement & Donoghue	2011	max	*lutescens*, not *sieboldii*
Tomentosa	Nakai	1921	min	*plicatum* + *hanceanum*
Nectarotinus	Donoghue & Clement	2014	min	*tinus* + *triphyllum* + *opulus* + *dilatatum*
Tinus	(Miller) C.B. Clarke	1880	min	*tinus* + *davidii*
Imbricotinus	Winkworth & Donoghue	2005	min	*triphyllum* + *opulus* + *diltatum*
Laminotinus	Donoghue & Clement	2014	max	*dilatatum*, not *opulus* or *triphyllum*
Sambucina	Kern	1951	max	*vernicosum*, not *acerifolium*, *cylindricum*, *diltatum*, or *kansuense*
Corisuccotinus	Donoghue & Clement	2014	max	*dilatatum*, not *vernicosum*
Coriacea	(Maxim.) Kern	1951	max	*vernicosum*, not *acerifolium*, *cylindricum*, *diltatum*, or *kansuense*
Succotinus	Winkworth & Donoghue	2005	max	*dilatatum*, not *acerifolium*
Opulus	(Tourn.) DeCandolle	1830	min	*edule* + *opulus*
Porphyrotinus	Winkworth & Donoghue	2005	min	*molle* + *triphyllum*
Mollotinus	Winkworth & Donoghue	2005	max	*molle*, not *triphyllum*
Oreinodentinus	Winkworth & Donoghue	2005	max	*triphyllum*, not *molle*
Dentata	(Maxim.) Hara	1983	max	*dentatum*, not *triphyllum*
Oreinotinus	(Oersted) Benth. et Hook.	1873	max	*triphyllum*, not *dentatum*

[1] All names refer to *Viburnum* species names.

[2] We use *V. nudum* as the specifier rather than *V. cassinoides* as *V. nudum* is the older name and therefore would take precedent if further study supports synonymizing these two names.

[3] We use *V. urceolatum* as the specifier rather than *V. taiwanianum* as *V. urceolatum* is the older name and therefore would take precedent if further study supports synonymizing these two names.

analysis. We have continued to use the suffixes *-viburnum* or *-tinus*. Where possible, the prefixes used refer to an apomorphy of the clade in question. Thus, we use *Nectarotinus* for the clade marked by extrafloral nectaries, *Laminotinus* for the clade marked by extrafloral nectaries embedded in the leaf lamina, and *Crenotinus* for the clade marked by curving (crenate) leaf teeth. In an attempt to convey geographic information, we use *Paleovaltinus* for the Old World component of *Valvatotinus.* In two cases, we chose names that referred to an aspect of the diversity of the group: *Regulaviburnum* for the "standard" or "normal" viburnums, as compared with the highly unusual *V. clemensiae*, and *Pluriviburnum* for the largest clade within *Regulaviburnum*, which is especially diverse morphologically. In two other cases, we combine elements of the names of included taxa: *Amplicrenotinus* for the clade including *V. amplificatum* and *Crenotinus*, and *Corisuccotinus* for the clade including *Coriacea* and *Succotinus*. Finally, *Perplexitinus* references our inability to identify a morphological character that marks this major, well-supported clade.

Table 2 shows the indented classification corresponding to the tree in Fig. 3 and also provides the author(s) of each name and the names of the specifiers (and their authors and publication dates) for their phylogenetic definitions. Two types of phylogenetic definition are used, both of which are intended to refer unambiguously to a specific node in the phylogeny (as opposed to the inclusion of stem lineages, or to clades stemming from the fixation of an apomorphic character state). As all of the specifiers are extant, all of the names refer to crown clades. Because most of the relationships under consideration here are now established with confidence, we have mainly used simple "minimum-clade" names taking the form: "the smallest clade containing specifier A and specifier B." In most cases only two specifiers are used, but in a few cases, where relationships are established with less certainty, three or four specifiers have been used. For example, the definition of *Regulaviburnum* specifies a member of each of the three major clades in the trichotomy in Fig. 3 (*Valvatotinus*, *Pseudotinus*, and *Pluriviburnum*).

In other cases, we used "maximum-crown-clade" definitions taking the form: "the largest crown clade containing specifier A, but not specifier C." For simplicity and consistency, we formulated reciprocal maximum crown-clade definitions for *Valvatotinus*, *Pseudotinus*, and *Pluriviburnum*, variously using *V. lentago* L., *V. lantanoides*, and *V. triphyllum* as internal and external specifiers. In other cases, we used maximum crown-clade definitions to cope with phylogenetic uncertainty. For example, our definition of *Euviburnum* copes with uncertainty about exactly which species will eventually straddle the basal split within this clade (e.g., *V. macrocephalum* Fortune, as shown in Fig. 2, or one or more of several species, e.g., *V. utile* Hemsl., that are situated outside of the well-supported core clade). In the special case of *Amplicrenotinus*, we used a maximum-crown-clade definition owing to an alternative placement of *V. amplificatum* in one of the gene trees (see above; should *Amplicrenotinus* become synonymous with *Crenotinus*, we prefer to retain *Crenotinus*). In general, we intend for our new names to be abandoned should the specified clade turn out not to exist. We note that we have not followed every rule for the establishment of clade names under the PhyloCode (http://www.phylocode.org); for instance, our names will need to be registered electronically when the PhyloCode formally takes effect.

Character evolution—Figure 4 shows parsimonious ancestral state reconstructions for each of the eight morphological characters noted, along with illustrations of their states. In most cases, these characters are invariant within the major named clades at the tips of the tree; multiple colors are used in cases of minor variation within a terminal and do not represent polymorphism within a species except as noted below. ML inferences (data not shown) are generally consistent with the MP results when branch lengths are treated as equal (set to 1) and when we consider alternative resolutions of polytomies and alternative scorings for the polymorphic tips in Fig. 4. Specifically, there is generally strong support with ML (proportional likelihood > 0.95) for the state assigned by MP, and ML never positively favors (proportional likelihood > 0.50) an alternative state assignment. In some cases where parsimony is equivocal in Fig. 4, ML results provide marginally better support for one of the alternative assignments. Examples of this will be detailed in what follows, in addition to minor differences in MP vs. ML reconstructions in a few cases. We wish to highlight that the use of our new phylogenetic nomenclature greatly expedites the following discussion.

(A) Bud form—Viburnum has long been noted for the presence of naked buds in some species (e.g., *V. lantanoides* in eastern North America; widely cultivated Asian species, such as *V. rhytidophyllum* and *V. carlesii* Hemsl.). In plants with naked buds, the outer pair of organs in the bud expand into fully developed leaves, in contrast with most viburnums in which there are differentiated bud scales that dehisce when the shoot expands (Cross, 1937, 1938). Based on this fundamental distinction, the "naked" condition is somewhat more widespread than once imagined and includes species in which the organs forming the outer envelope are not especially leaf-like in bud. For example, within the *Lentago* clade, *V. nudum* and *V. cassinoides* produce buds in which what appear to be the bud scales instead generally expand into normal vegetative leaves. In contrast, the related *V. lentago* produces bud scales that typically fall off as the shoot expands, though in this case various degrees of intermediacy may be observed. Likewise, although *V. tinus* and its relatives appear to have bud scales, and these sometimes fall off, they can and do often expand into normal (though sometimes smaller) leaves; consequently, we score the *Tinus* clade as polymorphic (Fig. 4A). As noted already, this interpretation is at odds with the use of the name *Imbricotinus* for the major clade including *Tinus*, and we have taken this opportunity to shift the application of this name to a less inclusive clade that does produce dehiscent scales. Finally, on the basis of our field studies in Southeast Asia, we score *V. punctatum* as having naked buds.

These new observations, placed in the context of our phylogeny, suggest the novel possibility that the first viburnums had naked buds. The highly divergent *V. clemensiae*, with its two pairs of bud scales, as well as the presence of bud scales in *Sambucus*, complicates this interpretation for *Viburnum* as a whole, but the *Regulaviburnum* clade could have originated with naked buds, in which case there were at least three shifts to scaly buds within it (Fig. 4A). It is likely that one pair of bud scales was ancestral within *Lutescentia*, with increases to two (and as many as four) pairs of scales in several species of *Solenotinus* in the Himalayan region (e.g., *V. grandiflorum*). The directionality is less clear in the *Imbricotinus* clade; however, if having one pair of scales in *Sambucina*, *Coriacea*, and possibly *Oreinotinus* is ancestral, then there were several shifts to two or more pairs of bud scales (e.g., 3–4 in *V. ellipticum* Hook.). The *Opulus* clade is noteworthy for the fusion of the outer bud scales into a thickened cap-like structure.

(B) Leaf margins—Schmerler et al. (2012) documented two major leaf syndromes within *Viburnum*: elliptical, evergreen leaves with entire margins in lowland tropical and montane cloud forests and rounder, deciduous leaves with toothed margins in temperate and boreal forests. Although highly significant phylogenetic correlations among these traits were evident in their data set, the directionality of evolution was uncertain. Our analyses yield a clearer picture. It now appears that entire leaves may have been ancestral in *Viburnum* and that there were at least five (or possibly seven) independent originations of toothed margins (Fig. 4B), often corresponding closely with a shift into temperate or boreal forests. We note, however, that while MP favors the retention of entire leaves along the backbone of the tree (Fig. 4), ML with molecular branch lengths is equivocal (ca. 0.5 proportional likelihoods) along the backbone when all polymorphic tips are coded as entire and slightly favors toothed leaves when all polymorphic tips are coded as toothed.

This interpretation is concordant with consistent differences among the toothed clades in the form of the teeth themselves. For example, the fine serrations that originated within the *Lentago* clade (Fig. 4B, *V. lentago*) differ from the coarse dentations characteristic of *Porphyrotinus* species (Fig. 4B, *V. dentatum*). Also, although the difference is subtle, the teeth in *Crenotinus* (Fig. 4B, *V. plicatum*) are distinctly curved on the proximal edge as compared with the more symmetrical teeth in *Porphyrotinus*, and in *Pseudotinus* the margins are typically doubly serrate (Fig. 4B, *V. lantanoides*).

We note that resolution of the equivocal condition at the base of *Laminotinus* (near *Sambucina* and *Coriacea*) depends on the final disposition of the *Opulus* clade. Based on the great overall similarity of the leaves in *Sambucina* and *Coriacea* to tropical species scattered elsewhere in the tree, we suspect that these

have retained their entire margins. However, we also note that teeth appear to have been almost completely lost several times independently within *Succotinus* [e.g., *V. japonicum* (Thumb.) C.K. Spreng, *V. sempervirens* K. Koch] apparently associated with shifts from colder temperate forests into warmer temperate or subtropical forests. This same transition from dentate to entire margins took place independently as *Oreinotinus* radiated into the cloud forests of Latin America.

(C) Inflorescence form—Viburnum inflorescences are umbel-like in ~140 species and panicle-like in ~24 species (Fig. 4C). The panicle form characterizes the *Solenotinus* clade (formerly section *Thyrsosma* in reference to the inflorescence). The panicle has generally been viewed as ancestral within *Viburnum* (e.g., Hara, 1983), with the umbel form derived by condensation of the internodes between opposite, decussate branches along the main axis, bringing the rays together at the apex of the stalk (highly reduced in some species, described as having sessile inflorescences).

When Kern described *V. clemensiae* in 1951, he placed it in *Solenotinus* based on its panicle-like inflorescence, one of the few reproductive features evident on the several specimens collected by that time (the flowers of *V. clemensiae* have only recently been described; Puff et al., 1997). Our analyses confirm previous phylogenetic studies (Clement and Donoghue, 2011) showing that the panicle-like inflorescence of *Solenotinus* was derived from an umbel-like ancestral condition, suggesting instead an evolutionary elongation of the central axis of the inflorescence. The panicle-like inflorescence in *V. clemensiae* (Fig. 5A, C) was clearly derived independently of that in *Solenotinus*, which accords well with evident structural and developmental differences between the inflorescences in these groups. In *Solenotinus* species the inflorescence is subtended by one or several pairs of leaves and is distinctly stalked, the primary branches are often distinctly opposite and decussate in arrangement and persist through fruit development and dispersal (Fig. 4C). In contrast, in *V. clemensiae*, in both staminate and carpellate individuals, the terminal central axis of the inflorescence is subtended by two pairs of bud scales, and the two lateral branches emerge in the axils of these scales (Fig. 5C). The side-branches on these axes are generally alternate and spirally arranged, and they typically disarticulate; i.e., lateral branches of the inflorescence abscise, leaving behind only the few axes bearing fruits in the carpellate inflorescences (Fig. 5B).

We have also observed paniculate inflorescences in some *V. lutescens* individuals and presume that these also occur, at least irregularly, in closely related species (e.g., *V. colebrookeanum* Wall. ex DC, *V. pyramidatum* Rehder). Indeed, both umbel-like and panicle-like inflorescences are sometimes produced by an individual *V. lutescens* plant (i.e., they are polymorphic within plants), though it is not yet clear how regularly this occurs or precisely how the different types are positioned on the plant. In any case, it is noteworthy that the capacity to produce paniculate inflorescences exists, and even varies within individual plants, and that this is observed in species that are closely related to the *Solenotinus* clade in which the paniculate condition has become completely fixed.

Finally, we note that inflorescence form also varies within the sister group of *Viburnum*, the Adoxoideae, and that *Sambucus*, like *Viburnum*, has both umbellate and paniculate forms (Donoghue et al., 2003). Here too, phylogenetic studies imply that the umbel form is ancestral and that the paniculate form evolved within *Sambucus* (Eriksson and Donoghue, 1997; Moore and Donoghue, 2009).

(D) Ruminate endosperm—Our expanded taxon sampling confirms the presence of ruminate endosperm of several types in *Viburnum*, the only clade within Adoxaceae that is known to have ruminate endosperm (Jacobs et al., 2010). What Jacobs et al. (2008) described as type 1 rumination reflects only the grooving of the endocarp and is not considered here. Of the species in which the wall of the seed coat is thickened and invaginated, *V. clemensiae* is characterized by many deep parallel invaginations, leaving very little and highly dissected endosperm (Fig. 5F; type 2A rumination of Jacobs et al., 2008). The remainder of the species with ruminate endosperm were placed by Jacobs et al. (2008) into two categories—type 2B in which the seed coat is formed by one layer of cells and the invaginations are narrow and relatively deep, and type 3 in which the seed coat is locally proliferated into thickened areas that form broader and more shallow invaginations.

In our sampling, we have encountered numerous intermediate conditions, to the point that we now see limited value in this distinction. We here score all species of the *Pseudotinus* and *Tinus* clades as having ruminate endosperm of varying thickness and depth (Fig. 4D). This condition clearly evolved separately in these two clades, providing an apomorphy for both. *Tinus* species tend to show more pronounced development of deep invaginations. In *Solenotinus* species, we have found variable expression of rumination but, where this does occur, localized regions of cell wall thickening rarely penetrate deeply into the endosperm. In comparing ML and MP reconstructions, if *V. erubescens* is scored as lacking ruminate endosperm, ML slightly favors (proportional likelihood 0.79) scoring the *Solenotinus* clade as lacking rumination. It is noteworthy that rumination tends to have evolved in fruits that are rounded in shape, with large internal volume. However, we note that the very large flattened seeds we have examined of *V. punctatum* have thickened and broadly invaginated seed coat walls, whereas those of the closely related *V. lepidotulum* lack rumination.

(E) Extrafloral nectaries—Weber et al. (2012) documented the presence of extrafloral nectaries (EFNs) of several types in *Viburnum* (Fig. 4E) and hypothesized a single origin of this trait within the clade, and a connection between EFNs and the production of mite-containing domatia. Our expanded sampling and the phylogenetic analyses reported here strongly support this conclusion, and, contrary to the expectation of some authors (e.g., Losos, 2011), provides a clear-cut example of a "functional" trait that shows no homoplasy and provides a clear-cut apomorphy for an old and species-rich clade within *Viburnum*. Furthermore, our analyses confirm the evolutionary sequence of events proposed by Weber et al. (2012), with EFNs probably first evolving at the base of the *Nectarotinus* clade through the modification of marginal leaf teeth near the base of the leaf blade.

EFNs appear to have moved from that original position toward, and then onto, the petiole where they are visited by ants in the boreal *Opulus* clade. The migration of EFNs onto the petiole occurred independently in the South American *V. toronis* Killip & A.C. Sm., nested deeply within the *Oreinotinus* clade. In the newly named *Laminotinus* clade, the EFNs are embedded in the leaf lamina, inward of the leaf margin. Finally,

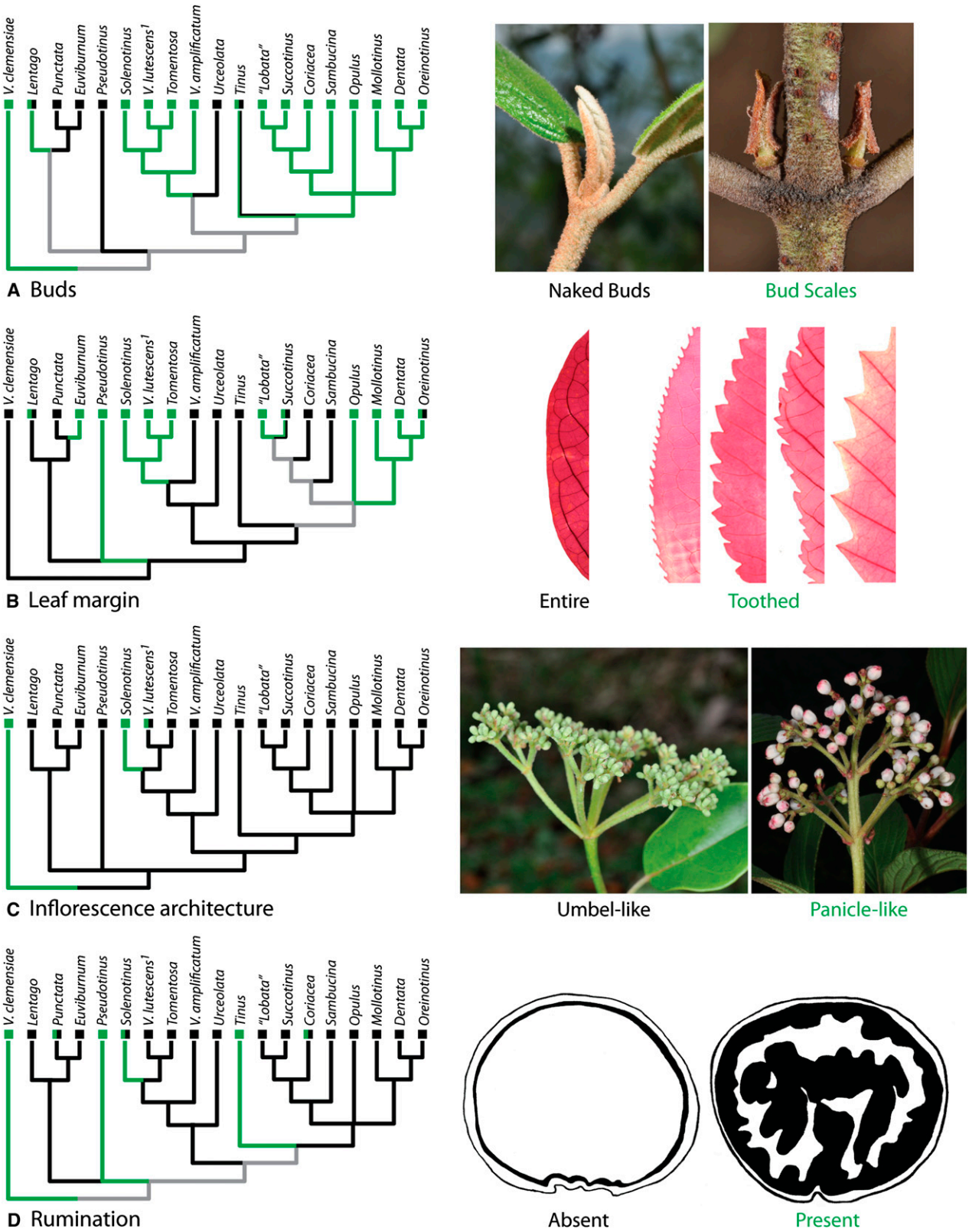
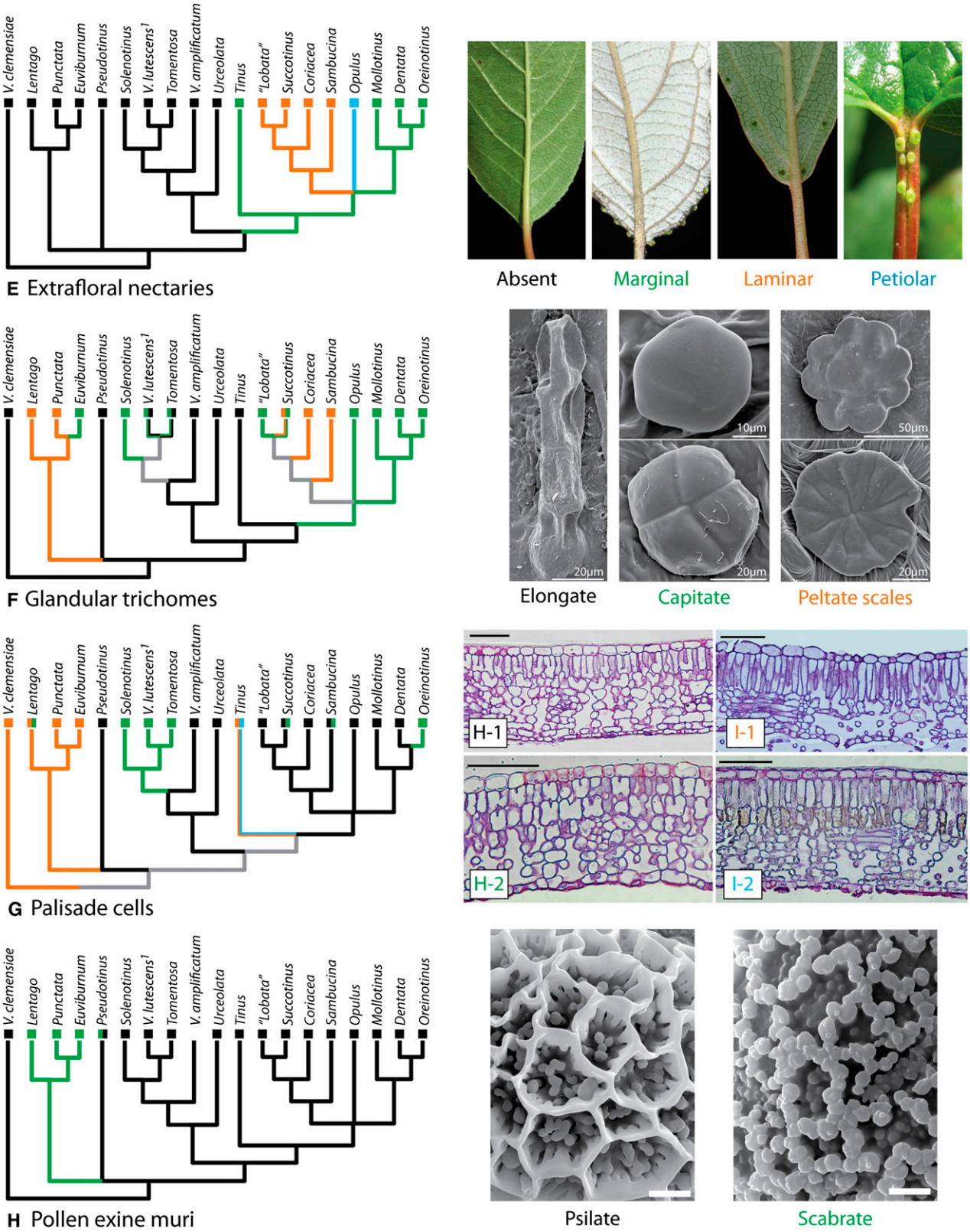


Fig. 4. Parsimony reconstructions of eight characters used to differentiate major groups of *Viburnum*. Characters A–D have been traditionally used, and E–G are more recently described characters. Illustrations of the character states are to the left, color coordinated with the states on the tree. (A) Buds. Naked: *V. congestum*; bud scales: *V. cylindricum*. (B) Leaf margins. Entire: *V. sambucinum*; toothed (left to right): *V. lentago*, *V. plicatum*, *V. lantanoides*, and *V. dentatum*. (C) Inflorescences. Umbel-like: *V. beccarii*; panicle-like: *V.* cf. *subalpinum*. (D) Ruminate endosperm. Absent: *V. prunifolium*; present: *V. cinnamomifolium*. In both drawings, the exterior line represents the endocarp, and the interior line represents the seed coat. In ruminate endosperm, the seed



coat is unevenly thickened. (E) Extrafloral nectaries. Absent: *V. rufidulum*; marginal: *V. anabaptista*; laminar: *V. cylindricum*; petiolar: *V. opulus*. (F) Glandular trichomes. Elongate: *V. clemensiae* (cells collapsed in SEM); capitate: *V. erosum* (top) and *V. acerifolium* (bottom); peltate scales: *V. beccarii* (top) and *V. cassinoides* (bottom). (G) Palisade cells (bar = 1 mm). H-1: *V. annamensis*; H-2: *V. hartwegii*; I-1: *V. lantanoides*; I-2: *V. propinquum*. (H) Pollen exine muri (bar = 2 µm). Psilate: *V. clemensiae*; scabrate: *V. lentago*. [1]Owing to uncertain resolution of species within *Lutescentia*, our scoring of *V. lutescens* reflects the states of that species alone.

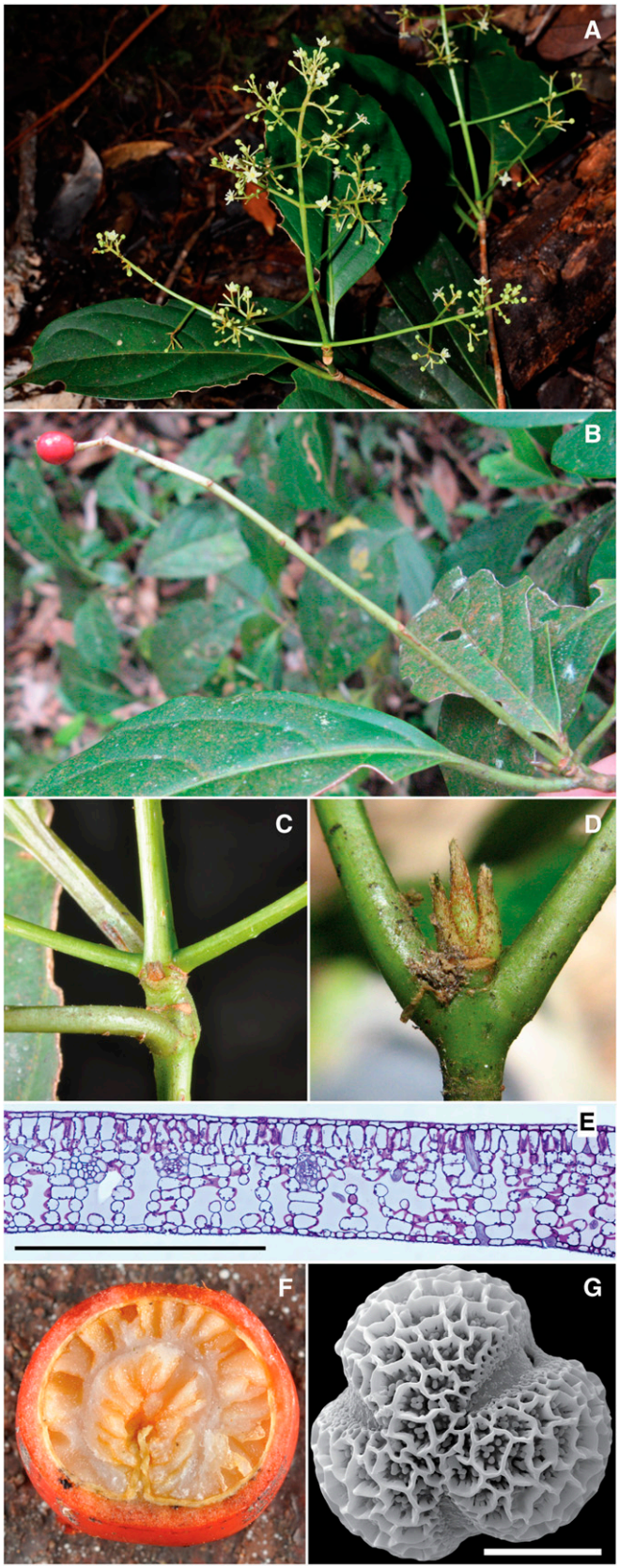


Fig. 5. *Viburnum clemensiae*. (A) Panicle-like inflorescence bearing carpellate flowers. (B) Disarticulated infructescence, with only axes bearing fruits. (C) Divergence into three axes at the base of the inflorescence. (D) Bud scales. (E) Palisade layer with one layer of I-cells (scale bar = 0.5 mm). (F) Ruminate endosperm showing deep invagination of the thin seed coat, leaving little endosperm. (G) Pollen grain showing Type 1A exine with smooth muri (scale bar = 10 μm).

we have discovered a novel condition in *V. platyphyllum* Merr. of the Philippines, in which large, possibly ant-tended EFNs are sometimes situated close to the upper (adaxial) midvein near the juncture with the petiole.

(F) Glandular trichomes—In addition to producing a wide variety of simple and stellate hairs, and in some cases densely pubescent stems, leaves, and buds (e.g., especially in the Asian *Euviburnum* clade, and parts of the Latin American *Oreinotinus*), minute glandular trichomes, generally reddish in color, have been noted in taxonomic accounts on the surfaces of the leaves, stems, inflorescences, and flowers. These glands have been cited as species-level characters (e.g., *V. punctatum*) and as distinguishing between subspecific taxa (e.g., *V. leiocarpum var. punctatum* P.S. Hsu). Although these glands presumably play a significant role in defense against herbivores, little attention has been paid to their function, form, or distribution.

Our SEM and light microscopic surveys demonstrate that these glands vary consistently in form and that, despite some homoplasy, tend to be conserved within major clades. We recognize three basic states (Fig. 4F). The most common form is short-stalked and upright, and with a capitate head of generally 2–4 cells. Fewer species produce larger, more elaborate peltate scales, in which the scale is often multicellular with more than four cells radiating from the central stalk. Finally, we especially note the presence of elongate glands lying parallel to the leaf surface, and closely appressed to it (Fig. 4F, "elongate"). These have a basal stalk portion with several segments and a head segment with 2–4 cells. This type of gland was described by Puff et al. (1997) in *V. clemensiae*. Although we at first considered this gland type to be unique to *V. clemensiae*, our SEM studies have revealed the presence of similar elongate glands in the *Pseudotinus*, *Tinus*, and *Urceolata* clades, as well as in *V. amplificatum* and some members of the *Lutescentia* clade.

The scattered distribution of elongate glands in members of several early-branching lineages suggests that this state may be ancestral for *Viburnum* (Fig. 4F), a possibility strengthened by our finding that similar glands are found in *Sambucus* (not shown). ML inferences using a tree with molecular branch lengths are consistent with MP except that when glands are assigned the presumably more ancestral state for the three polymorphic tips, the support for elongate and capitate glands is nearly equal at the *Nectarotinus* node. When polymorphic tips are scored with the derived state, capitate glands become slightly more likely for *Nectarotinus*, and elongate and capitate glands become almost equally likely for *Amplicrenotinus*. In any case, if elongate glands are a retained ancestral state, the other types may have been derived by shortening, becoming erect, and variously elaborating the head portion of the gland. These findings set the stage for more detailed anatomical studies and analyses of the chemical composition of the glands and their ecological role.

(G) Palisade anatomy—Chatelet et al. (2013) described and analyzed the function of four palisade types in *Viburnum* (Fig. 4G). Multiple evolutionary shifts among these types helped to identify significant physiological correlates. Here we emphasize that these leaf anatomical states mark several major clades. *Viburnum clemensiae* and members of the *Valvatotinus* clade produce one layer of I-shaped palisade cells (I-1, Fig. 5E). We know of only one exception in *Valvatotinus*, namely *V. rufidulum* Raf. within *Lentago*, which has two layers of H-cells (H-2, Fig. 5E) in the individuals that we have studied. I-shaped palisade cells evolved independently in the *Tinus* clade, within which a second layer of I-cells (I-2) was added in the core clade including *V. propinquum* Hemsl., *V. davidii* Franch., and *V. cinnamomifolium* Rehder, all of which have thicker leaves. The Asian *Crenotinus* clade is characterized by the production of two layers of H-cells (H-2), as is the entire *Oreinotinus* clade in Latin America. Some members of *Sambucina* and *Succotinus* also exhibit the H-2 condition, and in general, this is associated with thicker, often evergreen leaves and higher photosynthetic capacity (Chatelet et al., 2013). The H-1 state may be ancestral and retained in many lineages, which is consistent with the presence of H-cells in *Sambucus*, but we cannot entirely rule out that the I-1 condition is ancestral. However, under all scorings of polymorphic tips, ML slightly but consistently favors the H1 palisade type over other states along the backbone of *Regulaviburnum.*

(H) Pollen exine—Donoghue (1985) documented pollen exine diversity within *Viburnum* (also see Bohnke-Gutlein and Weberling, 1981). All are tricolpate with a semitectate, reticulate exine. In most species the muri (ridges) of the reticulum are psilate (smooth) on top (type 1A of Donoghue, 1985), while in others the muri are scabrate (bumpy; Fig. 4H). Donoghue (1985) distinguished between type 1B with a continuous reticulum and 1C with an irregular, discontinuous reticulum. These two conditions are lumped in Fig. 4H, where it is apparent that bumpy muri are characteristic of all species in *Valvatotinus*, providing additional morphological support for this clade. We note that type 1C is characteristic of the *Lentago* clade within *Valvatotinus*. Within *Pseudotinus*, *V. nervosum* D. Don exine is highly unusual. The reticulum appears to be broken into a series of large bumps, which do not themselves appear to be scabrate. This condition is scored as bumpy, but is likely to be an independently derived state, even if *Pseudotinus* turned out to be directly linked to *Valvatotinus*. Finally, we note that *V. clemensiae* (Figs. 4H, 5G) has prominent continuous and smooth reticulum (type 1A) and that smooth muri characterize *Sambucus* as well.

***Conclusions*—**Paired-end Illumina sequencing of the plastid genomes of 22 species has provided us for the first time with confident resolution of almost all of the deepest branching events within *Viburnum*. These relationships, and many more within the major clades, are supported in a combined analysis of 113 species. Two major phylogenetic problems remain, namely the exact positions of the *Pseudotinus* and *Opulus* clades. In addition, moving toward the tips of the tree, we remain uncertain about relationships in the vicinity of *V. lutescens*, about the existence of the *Lobata* clade, and about species-level relationships within several complexes, especially within the Asian *Succotinus* and *Solenotinus* clades and the Latin American *Oreinotinus* radiation. The resolution of these remaining phylogenetic problems requires new genomic approaches, especially sampling of the nuclear genome.

Over the past decade, we have progressively refined our understanding of *Viburnum* phylogeny to the point that a formal phylogenetic classification is now possible. Moreover, the increased precision provided by such a system is necessary as we expand the use of *Viburnum* in addressing general evolutionary and ecological questions. Here we have provided phylogenetic definitions for 30 clades that have previously been named—either formally under the ICN or informally—and we add nine new names to better communicate the deepest relationships within the tree. Our study provides an example both of the relative ease of providing a formal phylogenetic classification and, as exemplified by our discussion of character evolution, of the great practical utility of the increased precision provided by such a system.

Clarification of relationships at the base of *Viburnum* allows us to analyze the evolution of characters that vary at that level, including four that have been used previously in keys to the major groups and four that have been highlighted in our own recent studies. Although these show varying levels of homoplasy, they nevertheless collectively provide us with morphological evidence for the existence of major clades and a solid basis for distinguishing among the deep lineages. For example, our studies reveal many differences between *V. clemensiae* and *Regulaviburnum*, with *V. clemensiae* probably exhibiting the derived state in its inflorescence architecture and endosperm rumination. Likewise, it is now apparent that the otherwise heterogeneous *Valvatotinus* clade is marked by I-1 palisade, scabrate exine, and possibly peltate glands. *Nectarotinus* is supported by extrafloral nectaries, and the newly circumscribed *Imbricotinus* is marked by the evolution of bud scales and possibly capitate glands. The newly named *Crenotinus* clade is marked by the evolution of curved leaf teeth, bud scales, H-2 palisade, and possibly capitate glands. Several clades that have long been formally recognized at the section level are also marked by derived states of the characters considered here (e.g., *Pseudotinus* by doubly serrate leaf margins and ruminate endosperm; *Tinus* by ruminate endosperm and I-1/I-2 palisade; *Solenotinus* by paniculate inflorescences). At the same time, we are surprised that few, if any, derived morphological characters distinguish some of the deepest clades within *Viburnum*, including the newly named *Regulaviburnum* and *Perplexitinus* clades. To further test the existence of these deep clades, we have embarked on a study of multiple nuclear gene regions. At the same time, our development of a comprehensive morphological data matrix will aid in the demarcation of these clades and allow us to explore in detail the relationship between rates of molecular and morphological evolution.

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APPENDIX 1. GenBank accession numbers for the 22 species sequenced for whole plastid genomes. The following is a list of the gene regions and GenBank accession numbers assembled from whole plastid sequencing of 22 species. Twenty-two coding regions (from a total of 73) and 29 noncoding regions (from a total of 51) included in our analyses do not have GenBank accession numbers as they are either too short (>200 bp) to be accepted by GenBank, duplicate previously published data, or have been annotated as part of coding regions. However, the complete annotated nucleotide data set is available in TreeBASE (S15758) and Dryad (doi:10.5061/dryad.hh12b). Additionally, raw Illumina sequence data have been submitted to the Sequence Read Archive (SRA) of NCBI (SRP041815). The order of species for GenBank accession numbers is as follows: *V. acerifolium*, *V. amplificatum*, *V. carlesii*, *V. cassinoides*, *V. clemensiae*, *V. cylindricum*, *V. dentatum*, *V. dilatatum*, *V. erubescens*, *V. grandiflorum*, *V. lantanoides*, *V. lentago*, *V. lutescens*, *V. molle*, *V. opulus*, *V. plicatum*, *V. punctatum*, *V. sieboldii*, *V. taiwanianum*, *V. tinus*, *V. triphyllum*, *V. vernicosum*. Gene regions marked with an asterisk (*) indicate missing data for *V. vernicosum*.

Coding regions

atpA: KJ796313–KJ796334

atpB: KJ795390–KJ795411

atpE: KJ795676–KJ795697

atpF: KJ795061–KJ795082

atpH: KJ795500–KJ795521

atpI: KJ795941–KJ795962

ccsA: KJ795875–KJ795896

cemA: KJ795761–KJ795782

infA: KJ796248–KJ796269

*ndhA**: KJ794820–KJ794840

ndhA: KJ796335–KJ796355

ndhC: KJ796028–KJ796049

ndhD: KJ795588–KJ795609

*ndhE**: KJ796007–KJ796027

*ndhG**: KJ795281–KJ795301

*ndhH**: KJ796292–KJ796312

*ndhI**: KJ795719–KJ795739

ndhJ: KJ795324–KJ795345

petA: KJ795544–KJ795565

petB: KJ795193–KJ795214

petD: KJ795171–KJ795192

psaA: KJ796270–KJ796291

psaB: KJ795083–KJ795104

psaC: KJ795740–KJ795760

psbA: KJ795522–KJ795543

psbB: KJ794885–KJ794906

*psbC**: KJ795368–KJ795389

psbD: KJ796160–KJ796181

psbE: KJ796204–KJ796255

psbH: KJ795105–KJ795126

rpl2: KJ795654–KJ795675

rpl14: KJ795259–KJ795280

rpl16: KJ795897–KJ795918

rpl20: KJ794951–KJ794972

rpl22: KJ794907–KJ794928

rpl23: KJ795237–KJ795258

rpl33: KJ795434–KJ795455

rpoA: KJ795215–KJ795236

rpoB: KJ796226–KJ796247

rpoC1: KJ795149–KJ795170

rpoC1: KJ795985–KJ796006

rpoC2: KJ796116–KJ796137

rps2: KJ796050–KJ796071

rps3: KJ795963–KJ795984

rps4: KJ794841–KJ794862

rps8: KJ795412–KJ795433

rps11: KJ795853–KJ795874

rps14: KJ795456–KJ795477

*rps15**: KJ795698–KJ795718

rps16: KJ795478–KJ795499

rps18: KJ795610–KJ795631

rps19: KJ795809–KJ795830

ycf3: KJ795831–KJ795852

ycf4: KJ795017–KJ795038

Noncoding regions

atpB-rbcL: KJ796182–KJ796203

cemA-petA: KJ796138–KJ796159

ndhE-ndhG: KJ794973–KJ794994

psaI-ycf4: KJ794929–KJ794950

psbC-trnS$^{(UGA)}$: KJ795783–KJ795804

psbK-psbI: KJ794995–KJ795016

rpl16-rps3: KJ795346–KJ795367

rpl20-rps12: KJ795566–KJ795587

rps18-rpl20: KJ796072–KJ796093

trnF$^{(GAA)}$-ndhJ: KJ795302–KJ795323

trnL$^{(UAA)}$-trnF$^{(GAA)}$: KJ795039–KJ795030

trnL$^{(UAA)}$ intron: KJ796356–KJ796377

trnM$^{(CAU)}$-atpE: KJ795632–KJ795653

trnP$^{(GGG)}$-psaJ: KJ794863–KJ794884

trnQ$^{(UUG)}$-psbK: KJ795919–KJ795940

trnS$^{(GGA)}$-rps4: KJ796094–KJ796115

trnS$^{(UGA)}$-lhbA: KJ795127–KJ795148

trnV$^{(UAC)}$ intron: KJ796378–KJ796399

APPENDIX 2. Voucher information and GenBank accession data for 113 *Viburnum* species examined in this study. The majority of these data are from Clement and Donoghue (2011) and Chatelet et al. (2013). A few new sequences for ITS have been acquired since these studies, and those GenBank numbers are indicated in bold text. Species names are organized by clade following the indented format of Table 2. Herbarium abbreviations are as follows: A = Arnold Arboretum, Harvard University Herbaria, GH = Grey Herbarium, Harvard University, K = Kew Royal Botanic Gardens; MO = Missouri Botanical Garden, NY = New York Botanical Garden, WTU = University of Washington Herbarium; and YU = Yale University Herbarium. A hyphen (-) in the list of GenBank accessions indicates that we were unable to obtain the sequence.

Clade*. *Taxon; voucher specimen; herbarium; *trnH-psbA*; *rpl32-trnL*$^{(UAG)}$; ITS; *trnK*; *matK*; *rbcL*; *ndhF*; *trnC-ycf6*; *trnS-trnG*; *petB-petD*.

Viburnum*. *Viburnum clemensiae Kern; *J. Beaman 11781*; K; AY627387; HQ591878; AY265117; AY265163; HQ591569; HQ591714; HQ591648; HQ592122; EF490267; HQ591999.

***Regulaviburnum*.**

***Valvatotinus*.**

Lentago. ***Viburnum cassinoides*** L.; *Arnold Arboretum 874-85A, 0182773*; A; HQ592067; HQ591874; HQ591956; HQ591789; HQ591567; HQ591711; HQ591646; HQ592118; HQ591824; HQ591997. ***Viburnum elatum*** Benth.; *M.J. Donoghue 472*; YU; AY627394; HQ591887; AY265124; AY265170; HQ591578; HQ591721; -; -; EF490272; HQ592003. ***Viburnum lentago*** L.; *M.J. Donoghue & R.C. Winkworth 21*; YU; AY627406; HQ591905; AY265136; AY265182; HQ591598; HQ591739; HQ591670; HQ592148; EF490280; HQ592022. ***Viburnum nudum*** L.; *M.J. Donoghue NVI*; -; AY627410; HQ591915; AY265140; AY265186; HQ591608; HQ591749; HQ591677; HQ592156; EF490282; HQ592030. ***Viburnum prunifolium*** L.; *M.J. Donoghue & R.C. Winkworth 13*; YU; AY627413; HQ591922; AY265144; AY265190; HQ591615; HQ591756; HQ591683; HQ592163; EF490286; HQ592033. ***Viburnum rufidulum*** Raf.; *M.J. Donoghue & R.C. Winkworth 14*; YU; AY627415 ; HQ591927; AY265147; AY265193; HQ591620; HQ591761; HQ591687; HQ592167; EF490287; HQ592038.

Paleovaltinus.

Punctata. ***Viburnum lepidotulum*** Merr. & Chun; *Lau 27991*; A; HQ592083; HQ591906; -; HQ591800; HQ591599; HQ591740; -; -; -; -. ***Viburnum punctatum*** Buch.-Ham. Ex D. Don; *P.W. Sweeney et al. 2097*; YU; -; KF019866; **KJ795805**; KF019934; KF019748; KF019790; KF019768; KF019889; KF019913; KF019825.

Euviburnum. ***Viburnum bitchiuense*** Makino; *Arnold Arboretum living collection 1097-77A*; -; JX049467; JX049477; JX049448; JX049491; JX049451; JX049471; JX049459; JX049481; JX049495; JX049509. ***Viburnum burejaeticum*** Regel et Herder; *Arnold Arboretum living collection 375-95A*, *00223095*; A; JQ805297; JQ805472; -; JQ805552; JQ805231; JX049473; JX049463; JX049486; JX049500; JX049513. ***Viburnum carlesii*** Hemsl. Ex Forb. & Hemsl.; *M.J. Donoghue & R.C. Winkworth 24*; YU; AY627385; HQ591873; AY265115; AY265161; HQ591566; HQ591710; HQ591645; HQ592117; HQ591823; HQ591996. ***Viburnum cotinifolium*** D. Don; *M.J. Donoghue 267*; YU; KF019843; KF019864; KF019809; KF019932; KF019744; KF019787; KF019767; -; KF019908; KF019823. ***Viburnum lantana*** L.; *M.J. Donoghue & R.C. Winkworth 26*; YU; AY627404; HQ591902; AY265134; AY265180; HQ591595; HQ591736; HQ591667; HQ592145; EF490278; HQ592019. ***Viburnum macrocephalum*** Fortune; *M.J. Donoghue 101*; YU; HQ592086; HQ591911; EF462984; EF490247; HQ591604; HQ591745; HQ591673; HQ592153; HQ591842; HQ592027. ***Viburnum mongolicum*** (Pall.)Rehder; *M.J. Donoghue s.n.*; YU; HQ592087; HQ591914; EF462985; EF490248; HQ591607; HQ591748; HQ591676; HQ592155; HQ591844; HQ592029. ***Viburnum rhytidophyllum*** Hemsl. Ex Forb. & Hemsl.; *M.J. Donoghue & R.C. Winkworth 8*; YU; HQ592092; HQ591925; AY265146; AY265192; HQ591618; HQ591759; HQ591685; HQ592166; HQ591850; HQ592036. ***Viburnum schensianum*** Maxim.; *Boufford et al. 26082*; A; HQ592094; HQ591929; HQ591975; HQ591808; HQ591622; HQ591763; HQ591689; HQ592169; HQ591851; HQ592040. ***Viburnum utile*** Hemsl.; *Egolf 2336-E; cultivated plant*; AY627424; HQ591945; AY265156; AY265202; HQ591638; HQ591778; HQ591698; HQ592184; EF490291; HQ592054. ***Viburnum veitchii*** C.H. Wright; *D. Bouffourd et al. 27597*; A; HQ592106; HQ591946; HQ591985; HQ591817; HQ591639; HQ591779; HQ591699; -; HQ591861; HQ592055.

Pseudotinus. ***Viburnum furcatum*** Blume ex Hook.f. & Thomson; *Tsugaru & Takashi 19958*; MO; AY627399; HQ591893; AY265129; AY265175; HQ591585; HQ591728; HQ591658; HQ592136; EF490275; HQ592010. ***Viburnum lantanoides*** Michx.; *M.J. Donoghue & R.C. Winkworth 2*; YU; AY627405; HQ591903; AY265135; AY265181; HQ591596; HQ591737; HQ591668; HQ592146; EF490279; HQ592020. ***Viburnum nervosum*** D. Don; *D. Boufford et al. 27388*; A; AY627388; HQ591880; AY265118; AY265164; HQ591571; HQ591716; HQ591649; HQ592124; EF490268; -. ***Viburnum sympodiale*** Graebn.; *Lai & Shan 4529*; MO; HQ592100; HQ591937; EF462988; EF490252; HQ591630; HQ591770; -; HQ592177; EF490289; HQ592046.

Pluriviburnum.

Perplexitinus.

Urceolata. ***Viburnum taiwanianum*** Hayata; *W.-H. Hu et al. 2186*; MO; HQ592101; HQ591938; EF462989; EF490253; HQ591631; HQ591771; -; HQ592178; HQ591855; HQ592047. ***Viburnum urceolatum*** Siebold & Zucc.; *M.J. Donoghue NVI*; -; AY627423; HQ591944; AY265155; AY265201; HQ591637; HQ591777; HQ591697; -; HQ591860; HQ592053.

Amplicrenotinus. ***Viburnum amplificatum*** J. Kern; *P.W. Sweeney et al. 2149*; YU; KF019850; KF019871; **KJ795806**; KF019939; KF019753; KF019795; KF019773; KF019894; KF019918; KF019830.

Crenotinus.

Solenotinus. ***Viburnum awabuki*** Hort.Berol. Ex K. Koch; *Liu 141*; A; HQ592060; HQ591867; HQ591951; HQ591783; HQ591560; HQ591704; -; HQ592111; -; HQ591990. ***Viburnum brachybotryum*** Hemsl.; *NVI*; -; HQ592064; -; HQ591954; HQ591787; -; -; -; -; -; -. ***Viburnum chingii*** P.S. Hsu; *Bartholomew et al. 973*; A; HQ592069; HQ591876; HQ591958; -; -; HQ591712; -; HQ592120; -; -. ***Viburnum corymbiflorum*** P.S. Hsu & S.C. Hsu; *Gao 1706*; A; HQ592072; HQ591882; HQ591961; -; HQ591573; -; -; HQ592126; -; -. ***Viburnum erubescens*** Wall; *D. Boufford et al. 27190*; A; AY627397; HQ591889; AY265127; AY265173; HQ591581; HQ591724; HQ591655; HQ592133; HQ591831; HQ592006. ***Viburnum farreri*** Stearn; *M.J. Donoghue & R.C. Winkworth 18*; YU; AY627398; HQ591890; AY265128; AY265174; HQ591582; HQ591725; HQ591656; HQ592134; EF490274; HQ502007. ***Viburnum foetens*** Decne.; *M.J. Donoghue 270*; YU; KF019851; KF019872; KF019813; KF019940; KF019754; KF019796; KF019774; KF019895; KF019919; KF019831. ***Viburnum grandiflorum*** Wall. Ex DC; *M.J. Donoghue 271*; YU; KF019852; KF019873; KF019814; KF019941; KF019755; KF019797; KF019775; KF019896; KF019920; KF019832. ***Viburnum henryi*** Hemsl.; *M.J. Donoghue 272*; YU; KF019853; KF019874; KF019815; KF019942; KF019756; KF019798; KF019776; KF019897; KF019921; -. ***Viburnum odoratissimum*** Ker-Gawl.; *R. Olmstead 118*; WTU; AY627411; HQ591916; AY265141; AY265187; HQ591609; HQ591750; HQ591678; HQ592157; HQ591845; -. ***Viburnum oliganthum*** Batalin; *D. Bouffourd et al. 27175*; A; HQ592088; HQ591917; HQ591971; HQ591804; HQ591610; HQ591751; -; HQ592158; HQ591846; -. ***Viburnum sieboldii*** Miq.; *M.J. Donoghue & R.C. Winkworth 3*; YU; AY627417; HQ591932; AY265149; AY265195; HQ591625; HQ591766; HQ591691; HQ592172; HQ591853; HQ592042. ***Viburnum subalpinum*** Hand.-Mazz.; *Heng 11878*; GH; HQ592098; HQ591934; HQ591979; HQ591811; HQ591627; HQ591768; -; HQ592174; -; HQ592044. ***Viburnum suspensum*** Lindl.; *M.J. Donoghue & R.C. Winkworth 36*; YU; AY627419; HQ591936; AY265151; AY265197;

HQ591629; HQ591769; HQ591692; HQ592176; HQ591854; HQ592045. ***Viburnum taitoense*** Hayata; *M.J. Donoghue & K-F. Chung 1941*; YU; KF019854; KF019875; KF019816; KF019943; KF019757; KF019799; KF019777; KF019898; KF019922; KF019833.

Lutescentia. ***Viburnum colebrookeanum*** Wall. Ex DC; *Parker 3220*; A; HQ592070; HQ591879; HQ591959; HQ591791; HQ591570; HQ591715; -; HQ592123; -; HQ592000. ***Viburnum lutescens*** Blume; *Wu et al. WP531*; A; -; HQ591909; HQ591969; HQ591802; HQ591602; HQ591743; HQ591672; HQ592151; HQ591841; HQ592025.

Tomentosa. ***Viburnum plicatum*** Thunberg; *M.J. Donoghue & R.C. Winkworth 10*; YU; AY627412; HQ591920; AY265143; AY265189; HQ591613; HQ591754; HQ591681; HQ592161; EF490285; HQ592032.

Nectarotinus.

Tinus. ***Viburnum atrocyaneum*** C.B. Clarke; *D. Boufford et al. 34956*; A; HQ592059; HQ591866; HQ591950; HQ591782; HQ591559; HQ591703; HQ591642; HQ592110; HQ591820; HQ591989. ***Viburnum calvum*** Rehder; *Li & Soukup 934*; A; HQ592066; HQ591872; HQ591955; HQ591788; HQ591565; HQ591709; HQ591644; HQ592116; JX049508; HQ591995. ***Viburnum cinnamomifolium*** Rehder; *R. Olmstead 120*; WTU; AY627386 ; HQ591877; AY265116; AY265162; HQ591568; HQ591713; HQ591647; HQ592121; HQ591826; HQ591998. ***Viburnum davidii*** Franchet; *M.J. Donoghue 269*; YU; KF019862; KF019883; KF019821; KF019951; KF019765; KF019807; KF019785; KF019906; KF019930; KF019841. ***Viburnum propinquum*** Hemsl.; *M.J. Donoghue 100*; YU; HQ592090; HQ591921; EF462987; EF490250; HQ591614; HQ591755; HQ591682; HQ592162; -; -. ***Viburnum rigidum*** Vent.; *Stearn 1116*; A; HQ592093; HQ591926; HQ591974; HQ591807; HQ591619; HQ591760; HQ591686; -; -; HQ592037. ***Viburnum tinus*** L.; *M.J. Donoghue & R.C. Winkworth 35*; YU; AY627420; HQ591940; AY265152; AY265198; HQ591633; HQ591773; HQ591693; HQ592180; HQ591857; HQ592049.

Imbricotinus.

Laminotinus.

Sambucina. ***Viburnum beccarii*** Gamble; *P.W. Sweeney et al. 2106*; YU; KF019842; KF019863; KF019808; KF019931; KF019743; KF019786; KF019766; KF019884; KF019907; KF019822. ***Viburnum hispidulum*** J. Kern; *P.W. Sweeney et al. 2136*; YU; KF019846; KF019867; -; KF019935; KF019749; KF019791; KF019769; KF019890; KF019914; KF019826. ***Viburnum inopinatum*** Craib.; *P.W. Sweeney et al. 2091*; YU; KF019847; KF019868; **KJ795808**; KF019936; KF019750; KF019792; KF019770; KF019891; KF019915; KF019827. ***Viburnum sambucinum*** Reinw. Ex Blume; *P.W. Sweeney et al. 2100*; YU; KF019848; KF019869; KF019811; KF019937; KF019751; KF019793; KF019771; KF019892; KF019916; KF019828. ***Viburnum vernicosum*** Gibbs; *P.W. Sweeney et al. 2123*; YU; KF019849; KF019870; KF019812; KF019938; KF019752; KF019794; KF019772; KF019893; KF019917; KF019829. ***Viburnum ternatum*** Rehder; *Bartholomew et al. 2268*; A; HQ592102; HQ591939; HQ591981; HQ591813; HQ591632; HQ591772; -; HQ592179; HQ591856; HQ592048.

Corisuccotinus. ***Viburnum acerifolium*** L.; *M.J. Donoghue & R.C. Winkworth 27*; YU; AY627384; HQ591863; AY265114; AY265160; HQ591557; HQ591701; HQ591641; HQ592108; HQ591819; HQ591987. ***Viburnum kansuense*** Batalin; *D. Boufford et al. 27416*; A; AY627403; HQ591901; AY265133; AY265179; HQ591594; HQ591735; HQ591666; HQ592144; EF490276; HQ592018. ***Viburnum orientale*** Pall.; *Merello et al. 2291*; MO; HQ592089; HQ591919; EF462986; EF490249; HQ591612; HQ591753; HQ591680; HQ592160; EF490284; HQ592031.

Coriacea. ***Viburnum coriaceum*** Blume; *L. Averyanov et al. VH3300*; MO; HQ592071; HQ591881; HQ591960; HQ591792; HQ591572; HQ591717; HQ591650; HQ592125; -; HQ592001. ***Viburnum cylindricum*** Buch.-Ham. ex D. Don; *D. Boufford et al. 29342*; A; AY627389; HQ591883; AY265119; AY265165; -; -; -; HQ592127; EF490269; -. ***Viburnum hebanthum*** Wight & Arn.; *J. Klackenberg 32*; NY; HQ592076; HQ591895; -; HQ591795; HQ591587; HQ591729; HQ591660; HQ592138; HQ591833; HQ592012.

Succotinus. ***Viburnum adenophorum*** W.W. Sm.; *Boufford & Bartholomew 24402*; A; HQ592057; HQ591864; HQ591948; HQ591781; HQ591558; HQ591702; -; HQ592109; yes; HQ591988. ***Viburnum annamensis*** Fukouoka; *P.W. Sweeney et al. 2094*; YU; KF019855; KF019876; **KJ795807**; KF019944; KF019758; KF019800; KF019778; KF019899; KF019923; KF019834. ***Viburnum betulifolium*** Batalin; *D. Boufford et al. 29335*; A; HQ592061; HQ591868; -; HQ591784; HQ591561; HQ591705; -; HQ592112; -; HQ591991. ***Viburnum brachyandrum*** Nakai; *Mizushima 568*; A; HQ592063; HQ591870; HQ591953; HQ591786; HQ591563; HQ591707; -; HQ592114; HQ591821; HQ591993. ***Viburnum cf. corylifolium*** Hook.f. & Thomson; *D. Chatelet 103-99A*; A; JX049469; JX049479; KF019817; JX049493; JX049453; JX049475; JX049460; JX049483; JX049497; JX049511. ***Viburnum dilatatum*** Thunberg; *M.J. Donoghue & R.C. Winkworth 19*; YU; AY627392; HQ591885; AY265122; AY265168; HQ591575; HQ591719; HQ591652; HQ592129; HQ591828; -. ***Viburnum erosum*** Thunberg; *M.J. Donoghue & R.C. Winkworth 16*; YU; AY627396; HQ591888; AY265126; AY165172; HQ591580; HQ591723; HQ591654; HQ592132; EF490273; HQ592005. ***Viburnum flavescens*** W.W. Sm.; *D. Boufford et al. 32758*; A; HQ592074; HQ591891; HQ591962; HQ591794; HQ591583; HQ591726; HQ591657; -; JX049505; HQ592008. ***Viburnum foetidum*** **var.** ***rectangulatum*** (Graebn.) Rehder; *M.J. Donoghue & K-F. Chung 1942*; YU; KF019856; KF019877; KF019818; KF019945; KF019759; KF019801; KF019779; KF019900; KF019924; KF019835. ***Viburnum formosanum*** Hayata; *M.J. Donoghue & J.M. Hu 2007*; YU; KF019857; KF019878; -; KF019946; KF019760; KF019802; KF019780; KF019901; KF019925; KF019836. ***Viburnum hupehense*** Rehder; *Bartholomew et al. 1286*; A; HQ592077; HQ591896; HQ591964; HQ591796; HQ591588; HQ591730; HQ591661; HQ592139; HQ591834; HQ592013. ***Viburnum ichangense*** Rehder; *Bartholomew et al. 1889*; A; HQ592078; HQ591897; HQ591965; HQ591797; HQ591589; HQ591731; HQ591662; HQ592140; HQ591835; HQ592014. ***Viburnum integrifolium*** Hayata; *M.J. Donoghue & K-F. Chung 1946*; YU; KF019858; KF019879; -; KF019947; KF019761; KF019803; KF019781; KF019902; KF019926; KF019837. ***Viburnum japonicum*** Spreng; *NVI*; YU; AY627401; HQ591899; AY265131; AY265177; HQ591592; HQ591733; HQ591664; HQ592143; HQ591837; HQ592016. ***Viburnum luzonicum*** Rolfe; *Shen 673*; A; HQ592085; HQ591910; HQ591970; HQ591803; HQ591603; HQ591744; JX049466; HQ592152; JX049507; HQ592026. ***Viburnum melanocarpum*** Hsu in Chen et al.; *M.J. Donoghue & R.C. Winkworth 12*; YU; AY627408 ; HQ591912; AY265138; AY265184; HQ591605; HQ591746; HQ591674; -; HQ591843; HQ502028. ***Viburnum mullaha*** Buch.-Ham. Ex D.Don; *M.J. Donoghue 274*; YU; KF019859; KF019880; KF019819; KF019948; KF019762; KF019804; KF019782; KF019903; KF019927; KF019838. ***Viburnum parvifolium*** Hayata; *M.J. Donoghue & K-F. Chung 1953*; YU; KF019860; KF019881; KF019820; KF019949; KF019763; KF019805; KF019783; KF019904; KF019928; KF019839. ***Viburnum sempervirens*** K. Koch; *Hu & But 21891*; A; HQ592095; HQ591930; HQ591976; HQ591809; HQ591623; HQ591764; -; HQ592170; -; -. ***Viburnum setigerum*** Hance; *M.J. Donoghue 102*; YU; HQ592096; HQ591931; HQ591977; EF490251; HQ591624; HQ591765; HQ591690; HQ592171; HQ591852; HQ592041. ***Viburnum tashiroi*** Nakai; *M.J. Donoghue s.n.*; YU; KF019861; KF019882; -; KF019950; KF019764; KF019806; KF019784; KF019905; KF019929; KF019840. ***Viburnum wrightii*** Miquel; *Yonekura 1362*; A; HQ592107; HQ591947; HQ591986; HQ591818; HQ591640; HQ591780; HQ591700; HQ592185; HQ591862; HQ592056.

Opulus. ***Viburnum edule*** Raf.; *NVI*; -; AY627393; -; AY265123; AY265169; HQ591577; HQ591720; -; -; EF490271; -. ***Viburnum koreanum*** Nakai; *H. Yamaji 5170*; MO; HQ592081; -; EF462983; EF490246; -; -; -; -; EF490277; -. ***Viburnum opulus*** L.; *W.L. Clement 250*; YU; -; HQ591918; HQ591972; HQ591805; HQ591611; HQ591752; HQ591679; HQ592159; HQ591847; -. ***Viburnum sargentii*** Koehne; *M.J. Donoghue & R.C. Winkworth 17*; YU; AY627416; HQ591928; AY265148; AY265194; HQ591621; HQ591762; HQ591688; HQ592168; EF490288; HQ592039. ***Viburnum trilobum*** Marshall; *Arnold Arboretum 22900A*, *0174487*; AA; HQ592104; HQ591942; HQ591983; HQ591815; HQ591635; HQ591775; HQ591695; HQ592182; EF490290; HQ592051.

Porphyrotinus.

Mollotinus. ***Viburnum bracteatum*** Rehder; *Arnold Arboretum 1067-87A, 0227564*; A; HQ592065; HQ591871; -; KF019933; HQ591564; HQ591708; HQ591643; HQ592115; HQ591822; HQ591994. ***Viburnum ellipticum*** Hook.; *M.J. Donoghue NVI*; -; AY627395; -; AY265125; AY265171; HQ591579; HQ591722; HQ591653; HQ592131; HQ591830; HQ592004. ***Viburnum molle*** Michx.; *M.J. Donoghue & R.C. Winkworth 5*; YU; AY627409 ; HQ591913; AY265139; AY265185; HQ591606; HQ591747; HQ591675; HQ592154; EF490281; -. ***Viburnum rafinesquianum*** Schult.; *M.J. Donoghue & R.C. Winkworth 4*; YU; AY627414; HQ591924; AY265145; AY265191; HQ591617; HQ591758; HQ591684; HQ592165; HQ591849; HQ592035.

Oreinodentinus.

Dentata. ***Viburnum dentatum*** "2" L.; *M.J. Donoghue & R.C. Winkworth 33*; YU; AY627391; HQ591884; AY265121; AY265167; HQ591574; HQ591718; HQ591651; HQ592128; HQ591827; HQ592002. ***Viburnum recognitum*** Fernald; *Arnold Arboretum 1471-83B, 00192902*; A; JQ805337; JQ805507; JQ805189; JQ805585; JQ805261; JQ805387; JX049465; JX049490; JX049504; KF019824.

Oreinotinus. ***Viburnum acutifolium*** Benth.; *M.J. Donoghue 96*; YU; JQ805307; -; JQ805160; -; JQ805237; JQ805397; -; KF019885; -; -. ***Viburnum blandum*** C.V. Morton; *M.J. Donoghue 464*; YU; HQ592062; HQ591869; HQ591952; HQ591785; HQ591562; HQ591706; -; HQ592113; -; HQ591992. ***Viburnum caudatum*** Greenm.; *M.J. Donoghue 64*; YU; HQ592068; HQ591875; HQ591957; HQ591790; -; -; -; HQ592119; HQ591825; -. ***Viburnum costaricanum*** (Oerst.) Hemsl.; *M.J. Donoghue 85*; YU; JQ805482; JQ805164; JQ805564; -; -; -; -; KF019909; . ***Viburnum discolor*** Benth.; *M. Veliz et al. 35-99*; MO; JQ805314; JQ805485; JQ805166; -; JQ805241; JQ805402; -; KF019886; -; -. ***Viburnum disjunctum*** C.V. Morton; *M.J. Donoghue 700*; YU; KF019844; -; KF019810; -; KF019745; KF019788; -; KF019887; KF019910; -. ***Viburnum hartwegii*** Benth.; *M.J. Donoghue 486*; YU; AY627400; HQ591894; AY265130; AY265176; HQ591586; -; HQ591659; HQ592137; HQ591832; HQ592011. ***Viburnum jamesonii*** (Oerst.)Killip & A.C. Sm.; *P.W. Sweeney et al. 1636*; YU; HQ592080; HQ591898; HQ591966; HQ591798; HQ591591; HQ591732; HQ591663; HQ592142; HQ591836; HQ592015. ***Viburnum jucundum*** C.V. Morton; *M.J. Donoghue 244*; YU; AY627402; HQ591900; AY265132; AY265178; HQ591593; HQ591734; HQ591665; -; HQ591838; HQ592017. ***Viburnum lautum*** C.V. Morton; *M.J. Donoghue 72*; YU; HQ592082; HQ591904; HQ591967; HQ591799; HQ591597; HQ591738; HQ591669; HQ592147; HQ591839; HQ592021. ***Viburnum loeseneri*** Graebn.; *M.J. Donoghue 2547*; YU; HQ592084; HQ591908; HQ591968; HQ591801; HQ591601; HQ591742; -; HQ592150; -; HQ592024. ***Viburnum stellato-tomentosum*** (Oerst.) Hemsl.; *M.J. Donoghue 640*; YU; KF019845; KF019865; -; -; KF019747; KF019789; -; KF019888; KF019911; -. ***Viburnum stenocalyx*** Hemsl.; *M.J. Donoghue 60*; YU; HQ592097; HQ591933; HQ591978; HQ591810; HQ591626; HQ591767; -; HQ592173; KF019912; HQ592043. ***Viburnum sulcatum*** (Oerst.)Hemsl.; *M.J. Donoghue 207*; YU; HQ592099; HQ591935; HQ591980; HQ591812; HQ591628; -; -; HQ592175; -; -. ***Viburnum toronis*** Killip & A.C. Sm.; *P.W. Sweeney et al. 1799*; YU; HQ592103; HQ591941; HQ591982; HQ591814; HQ591634; HQ591774; HQ591694; HQ592181; HQ591858; HQ592050. ***Viburnum triphyllum*** Benth.; *P.W. Sweeney et al. 1783*; YU; HQ592105; HQ591943; HQ591984; HQ591816; HQ591636; HQ591776; HQ591696; HQ592183; HQ591859; HQ592052.