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Parallelism in Endocarp Form Sheds Light on Fruit Syndrome Evolution in *Viburnum*

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Abstract—All *Viburnum* species produce drupes with a hardened endocarp surrounding a single seed. Endocarp form varies greatly within *Viburnum*, and differences in shape have long been used to distinguish major subclades. Here we trace the evolution of *Viburnum* endocarp shape using morphometric analyses and phylogenies for 115 *Viburnum* species. Endocarp measurements were obtained from fruits sampled from herbarium specimens and from field collections, and shapes were analyzed using elliptical Fourier analysis. We infer that the first viburnums had flattened and grooved endocarps. Subsequently, there were multiple losses of grooving in conjunction with shifts to both highly flattened and nearly round endocarps. In several clades the parallel evolution of a derived endocarp shape was accompanied by changes in a suite of other fruit traits, yielding distinctive fruit syndromes likely related to bird dispersal. However, in other clades endocarp shapes similar to the ancestral form have been retained while other fruit traits (color, amount of flesh, nutritional content) have diverged. We quantify cases of parallel evolution in endocarp shape that cut across recognized fruit syndromes such as red, carbohydrate-rich fruits with flattened endocarps or blue, lipid-rich fruits with round endocarps. Our analyses now invite studies of function and the selective factors that have yielded the distinctive suites of fruit and seed traits that distinguish the major *Viburnum* lineages.

Keywords—Elliptical Fourier analysis, morphometrics, phylogeny.

The enormous diversity of fruit types has long been tied to the evolution of seed dispersal strategies. Animal dispersal, involving frugivorous birds and mammals (endozoochory), is practically synonymous with the production of fleshy propagules (Van der Pijl 1969). Variation among fleshy fruits with respect to color, texture, nutrition, and shape is determined by differences in the pericarp layers surrounding the seed. One type of fleshy fruit is the drupe, which generally has a single seed surrounded by a hardened endocarp that is differentiated from the fleshy layers. For plants with endocarps, this forms an additional protective layer around the seed (Dardick and Callahan 2014). While the precise role of endocarp morphology in relation to seed protection, dispersal, and germination is largely unknown, various conditions of the endocarp, including overall size and thickness, have been shown to affect seed removal and dispersal (Zhang and Zhang 2008). Aside from their functional significance, endocarp shapes have been important in taxonomic studies and in delimiting species and clades (e.g. Plunkett et al. 1996; Sattarian and van der Maesen 2006; Depypere et al. 2007; Wefferling et al. 2013; Koubouris et al. 2019). Likewise, fossilized endocarps are of great interest to paleobotanists for identification purposes (e.g. Dilcher and McQuade 1967; Boon et al. 1989; Rozefelds and Christophel 1996; Gottschling et al. 2002; Li et al. 2011). Yet, despite this interest from various quarters, there have been few detailed quantitative and comparative studies of endocarps and associated fruit traits conducted in a phylogenetic context.

Viburnum L. is a clade of approximately 165 species characterized by drupes that range in mature color from yellow to red to blue to black (Fig. 1). In his worldwide treatment of *Viburnum* in 1861, Oersted highlighted the value of endocarp shape in distinguishing between major groups of species, some of which he recognized at the time as separate genera. These distinctions have been well appreciated in more recent treatments (Rehder 1940; Hara 1983; Donoghue 1983a, 1983b; Yang and Malécot 2011). Jacobs et al. (2008) provided the first evolutionary perspective on endocarp morphology in *Viburnum*, identifying five broad categories of grooving. Using a phylogeny of the 17 species that were studied in detail, they inferred multiple transitions from an endocarp shape with grooving to a flattened or to a spherical endocarp with little or no grooving (Jacobs et al. 2008). Since then there have been significant improvements in our understanding of *Viburnum* phylogeny. A concerted effort to increase sampling and resolution, using a greatly expanded set of genetic markers, has resulted in a tree that includes one or more samples of nearly all ~165 species (Clement and Donoghue 2011; Clement et al. 2014; Spriggs et al. 2015; Landis et al. 2020). Additionally, an analysis of a suite of *Viburnum* fruit traits in a phylogenetic framework has documented the repeated evolution of two distinct 'fruit syndromes' (Sinnott-Armstrong et al. 2020). One syndrome includes species with blue fruit color, low moisture yet lipid-rich pulp, and rounded endocarps. The other major syndrome includes red-fruited species with high moisture yet carbohydrate-rich pulp, and flattened endocarps (Sinnott-Armstrong et al. 2020). This study documented correlations between basic endocarp shape (length and width measurements) and other fruit traits, but subtle differences in grooving patterns and overall endocarp form were not explored.

Here we further the study of endocarp evolution in *Viburnum* by incorporating 70% of extant species diversity. Treating endocarp shape as a continuous character and employing a tree-based analysis of convergence, we explore endocarp shape evolution in the context of a far more complete *Viburnum* phylogeny. We relate our findings to previous studies of endocarp morphology (Jacobs et al. 2008), revisit the fruit dispersal syndromes of Sinnott-Armstrong et al. (2020), and consider the significance of endocarp shape for *Viburnum* taxonomy.

Materials and Methods

Sampling—To examine variation in endocarp shape, we sampled 122 of the ca. 165 species of *Viburnum*, covering all major subclades (Appendix 1). Endocarps were sampled from dried and pickled fruits from field collections (P.W. Sweeney, W.L. Clement, and M.J. Donoghue) as well as dried

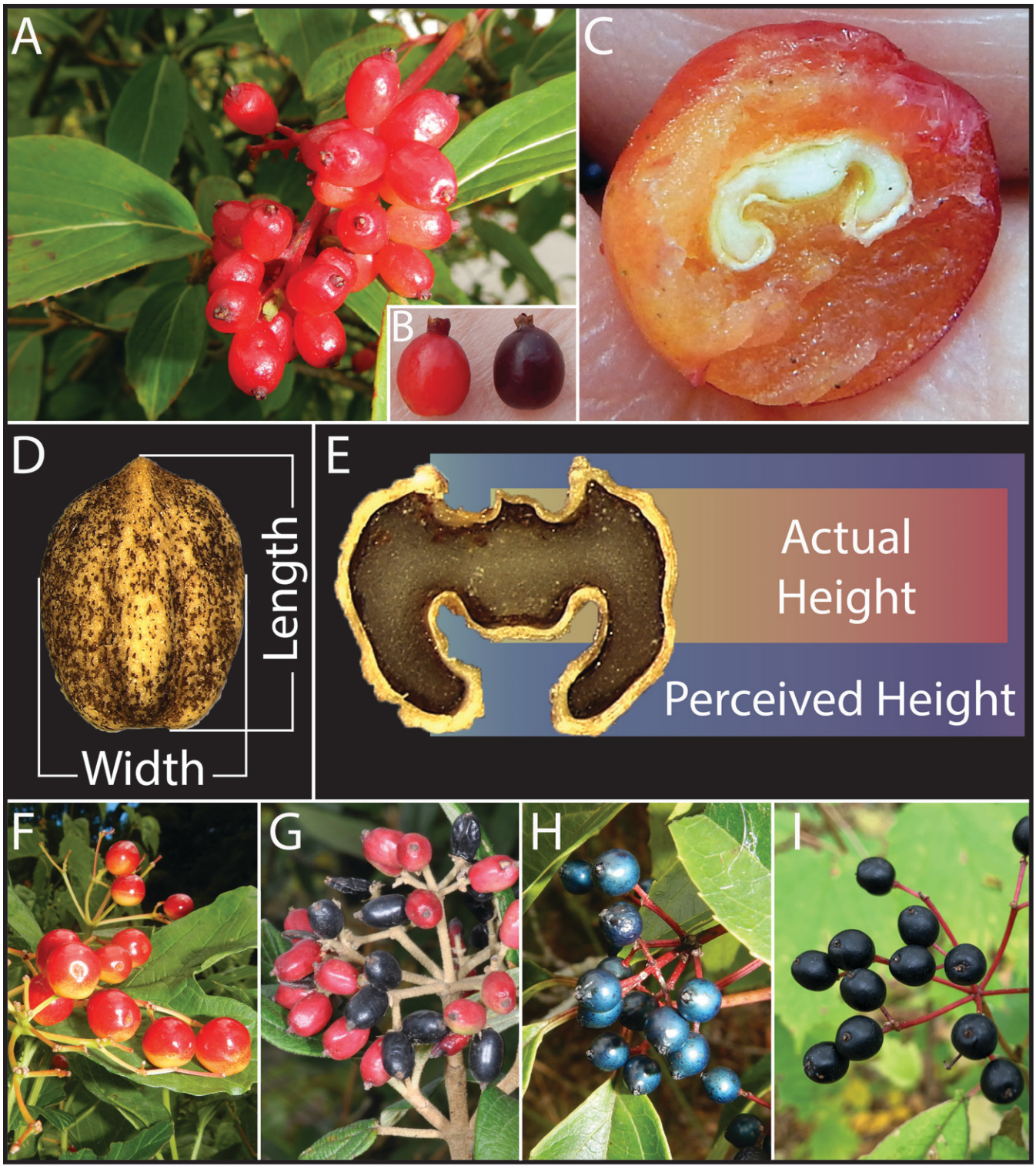

FIG. 1. Fruit and endocarp morphology in *Viburnum*. A. Infructescence of *V. erubescens* (Solenotinus). B. At maturity, the red fruits of *V. erubescens* turn black one at a time (sequential color development). C. Cross section of a *V. erubescens* fruit showing the endocarp and the white endosperm of the seed within. D. Width and length measurements made on whole endocarps. E. Two different height measurements taken from endocarps in cross-section: 'actual' height (red rectangle) and 'perceived' height (blue rectangle). F–I. Variation in *Viburnum* fruit color. F. Synchronous maturation of *V. opulus* fruits from yellow to red. G. Sequential maturation of the fruits of *V. chinshanense* from red to black. H. Metallic blue fruits of *V. propinquum*. I. Black fruits of *V. acerifolium*. Photo credits: M. J. Donoghue A–C, F, H, I; P. W. Sweeney G.

fruits from herbarium sheets at A, GH, and YU. Four species, from distantly related lineages within *Viburnum*, were chosen to explore intraspecific variation in endocarp shape: *V. dentatum* L. (Dentata), *V. prunifolium* L. (Lentago), *V. dilatatum* Thunb. (Succotinus), and *V. acerifolium* L. (Lobata). Approximately 10 fruits from each of five individuals were sampled for a total of 50 fruits per focal species. Fruits were sampled from The College of New Jersey, Ewing, New Jersey; the main campus of Yale University, New Haven, Connecticut; the Marsh Botanical Garden of Yale University, New Haven, Connecticut; and the Nayfield Preserve, Hopewell Township, New Jersey.

Our phylogenetic analysis of *Viburnum* included 115 of the 122 species for which endocarp data were collected. The seven species for which shape data were collected but insufficient molecular data were available are *V. fordiae* Hance, *V. hondurense* Standl., *V. ovatifolium* Rehder, *V. tengyuehense* (W.W.Sm.) P.S.Hsu, *V. ternatum* Rehder, *V. tiliaefolium* (Oerst.) Hemsl., and *V. tsangii* Rehder. Here we highlight our most recent *Viburnum* phylogeny based on cpDNA and nrITS sequences (see Landis et al. 2020). We also carried out all relevant analyses using a tree based largely on RAD-seq data (Landis et al. 2020). Although the tree topologies obtained in these analyses are similar in most respects, there are some important differences listed below, including alternative placements of *V. clemensiae* J.Kern, which has often been placed as sister to all other viburnums based largely on cpDNA data (Clement et al. 2014; Spriggs et al. 2015; but see Lens et al. 2016). For comparability, we pruned the Landis et al. (2020) RADseq-based tree to include the same 115 taxa as the cpDNA+nrITS dataset. All morphological data matrices and trees are available in Dryad (Clement et al. 2021).

***Sample Preparation and Imaging*—**As the endocarp is a hard, fibrous structure surrounding the seed, its form is well preserved on herbarium specimens from which the majority of our data were collected. Measurements of endocarps were made directly from digital images of herbarium and pickled collections using a Leica stereoscope outfitted with a 3.1 megapixel digital camera or from camera lucida drawings of dried endocarps. For pickled material, the exocarp and mesocarp were manually stripped from the fruit to expose the endocarp. For herbarium specimens, the fruit pulp generally dries to a relatively thin layer around the endocarp and is easily removed or distinguished by its color and texture from the endocarp. Endocarps were first photographed lying flat (i.e. with both the apex and base in view). The endocarps were then cut in cross section using a razor blade, positioned upright in clay and photographed in cross section with the dorsal side toward the top of the image. Camera lucida drawings representing the same set of photographs were drawn at a 9 × scale (except *V. lentago* drawn at 6×) and digitized to facilitate measuring. The dorsal and ventral sides of a *Viburnum* endocarp can readily be established in cross section by reference to a prominent vascular bundle (the "central bundle" of Wilkinson 1948) that runs from the bottom to the top of the ovary through the center of the mesocarp along the ventral side.

***Measurements of Endocarp Shape*—**Measurements were taken from the digital images and camera lucida drawings using ImageJ (Abramoff et al. 2004) and Leica Application Suite X (LASX) software (Leica Microsystems, Buffalo Grove, Illinois). 'Length' was measured as the distance from the apex to the farthest point at the base of the endocarp (Fig. 1D). 'Width' was measured as the distance between the farthest points along the lateral axis of the endocarp (Fig. 1D). As many endocarp shapes have a prominent ventral groove in their cross section, which effectively creates lateral "arms" of the endocarp that appear to curve and create a horseshoe shape (e.g. Solenotinus, Fig. 1C), we collected two different 'height' measurements. The first, 'perceived height,' was measured as the distance between the farthest points from the dorsal to the ventral side of the endocarp, i.e. taking into account any curvature (Fig. 1E). Then, 'actual height' was measured as the distance in the center of the cross section of the endocarp from the dorsal to the ventral side, i.e. ignoring any lateral curvature (Fig. 1E). In an endocarp that is flattened and not curved around a central groove, the perceived and the actual heights could be the same. The distribution of endocarp shape was examined using a scatterplot generated using R statistical software (R Core Team 2019), comparing the width/perceived height ratio against the length of the endocarp.

To calculate an approximate volume of an endocarp, we considered the shape to be best represented by an ellipsoid. We then applied the formula to calculate the volume of an ellipsoid ($4/3\pi abc$) using the length (a), width (b), and perceived height (c) measurements. This formula will somewhat overestimate volume for those endocarps with a central intrusion (e.g. Solenotinus or Dentata). However, given that endocarp shape is consistent within each major *Viburnum* clade, possible implications of this overestimate can be evaluated on a clade by clade basis.

***Elliptical Fourier Analysis of Endocarp Shape*—**To facilitate phylogenetic studies, we analyzed endocarp shape using elliptical Fourier analysis (EFA) as opposed to landmark or sliding-landmark approaches (Jacques and Zhou 2010); this allowed us to circumvent the lack of reliable, homologous landmarks (Wefferling et al. 2013). Using Adobe Photoshop CC 2014.2.1, digital images of individual endocarp cross sections were cropped and binarized such that the endocarp cross section was completely filled in using the smart selection tool, and the background was deleted to produce a black and white image.

EFA was performed using the Momocs package (Bonhomme et al. 2014) in R (R Core Team 2019) with the binarized images. The 50 samples for each of the four focal species for the intraspecific study (*V. acerifolium*, *V. dentatum*, *V. dilatatum*, and *V. prunifolium*) were analyzed separately to determine the extent of variation within a species. Then, EFA, as described below, was performed on the dataset including 122 species of *Viburnum*.

Within Momocs, the direction argument belonging to the coo_slidedirection function was set to north by default in the initial stages of scaling the images. At the start of the scaling step, Momocs would begin by placing the landmark in the center of the image and moving north until reaching the upper limit of the endocarp (e.g. dorsal side). Particularly in Solenotinus, where endocarps are horseshoe-like in shape, the initial landmark was often placed in a position in the image outside of the endocarp itself, below the ventral side of the endocarp. As the landmark moved north it would reach the lower limit (ventral side) rather than the upper limit (dorsal side) as it did on all other endocarp images. In these instances, the image of the endocarp would be inverted and cause the generation of a morphospace that included biologically impossible shapes. To correct for this problem, we resized and cropped the image of horseshoe shaped endocarps to ensure that the first landmark would land on the seed itself between the dorsal and ventral limits of the endocarp. The data were then used in a principal component analysis (PCA) using Momocs efourier function in R (R Core Team 2019).

***Phylogenetic Analyses*—**We assembled a data matrix for 115 *Viburnum* species including 10 gene regions (nrITS and nine plastid regions: *matK*, *ndhF*, *petB-petD*, *rbcL*, *rpl32-trnL*$^{(UAG)}$, *trnC-ycf6*, *trnH-psbA*, *trnK*, and *trnS-trnG*) obtained from the data used in reconstructing the most comprehensive *Viburnum* phylogeny published to date (Landis et al. 2020; Appendix 1). Gene regions were aligned individually using Muscle v. 3.8.31 (Edgar 2004). Partitionfinder v. 2.1.1 (Lanfear et al. 2012) was used to determine the best partitioning strategy for the 10 gene regions and corresponding best fit models of sequence evolution. For this cpDNA+nrITS-based analysis, *V. clemensiae* was used to root the tree based on prior studies using *Sambucus* L. species as outgroups (Donoghue et al. 2004; Winkworth and Donoghue 2005; Clement and Donoghue 2011; but see Lens et al. 2016).

Phylogenetic analyses were conducted in both a maximum likelihood (ML) and a Bayesian inference framework (BI). ML analyses were performed in Garli v. 2.0 (Zwickl 2006). ML analyses were repeated independently five times with each analysis iterated five times to ensure that likelihood scores were similar among runs. Additionally, ML bootstrap analyses with 500 replicates were performed using the same models of sequence evolution. BI analyses were run in MrBayes v. 3.2.6 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) for 40 million generations with four chains and model parameters among partitions unlinked. The posterior distribution was sampled every 1000 generations, and the convergence and burn-in were determined visually by inspecting plots of all parameters in Tracer v. 1.7 (Rambaut et al. 2018). The burn-in was removed prior to summarizing model parameters and sampling trees from the posterior distribution.

Analyses of endocarp evolution were also conducted on the maximum clade credibility tree topology of Landis et al. (2020) based on RADseq data, which was pruned to include just the 115 species in our cpDNA + nrITS dataset.

***Morphological Evolution*—**Continuous trait data pertaining to endocarp shape measurements obtained from the EFA, as well as volume estimations, were reconstructed on the 115-species tree with branch lengths based on the 10-gene cpDNA + nrITS data matrix (Landis et al. 2020). Ancestral character state analysis under ML was performed and visualized using the fastAnc function of the phytools package (Revell 2012) in R (R Core Team 2019). Using the RADseq tree without branch lengths (Landis et al. 2020), we reconstructed ancestral character states for the same traits under maximum parsimony in Mesquite v. 3.51 (Maddison and Maddison 2019).

A phylomorphospace was generated using APE (Paradis et al. 2004) and phytools (Revell 2012) packages in R (R Core Team 2019) using the 115-species *Viburnum* phylogeny reconstructed from the 10-gene data set and the morphospace generated from PC1 and PC2 from the EFA. Internal nodes were placed based on ancestral character state analysis using fastAnc on the first and second principal component scores.

***Quantifying Parallel Evolution*—**Having measured endocarp shape as a continuous trait, we were able to apply a tree-based approach to quantifying putative cases of parallel evolution that uses both phenotypic distances and the tree topology (Stayton 2015). For any two taxa hypothesized to have evolved in parallel, the inferred evolution through phenotypic space is likely to diverge before converging on a similar part of the phylomorphospace. To this end, using the metrics proposed by Stayton (2015), we calculated a convergence index, C1, that measures the amount of convergent evolution that has occurred based on the contemporary phenotypic distance between two selected species (i.e. the Euclidean distance between them in the phylomorphospace, D_{tip}) and the maximum distance attained anywhere along the branches that trace back to their most recent common

ancestor (D_{max}). This metric ranges from 0 to 1, with C1 approaching 1 when the two taxa being compared have evolved very similar endocarp shapes from very different parts of the phylomorphospace (Stayton 2015).

To explore parallel evolution of endocarp shape in light of phylogeny in *Viburnum*, we applied the C1 metric to three potential cases of parallel evolution based on generalized endocarp shapes that occur in more than one *Viburnum* clade: 1) compressed, non-undulating endocarps (e.g. Opulus and Lentago), 2) round endocarps with a prominent central intrusion (e.g. Solenotinus, Dentata, and Oreinotinus of northern Mexico), and 3) round endocarps with a very reduced central intrusion (including *V. clemensiae*, Tinus, and Oreinotinus of South America). We calculated C1 for all pairwise combinations among members of the putatively convergent clades using the convrat function in the convevol package (Stayton 2015) in R (R Core Team 2019) and averaged the results. Significance was assessed using the convratsig function in convevol (Stayton 2015) with 100 simulations.

Results

Intraspecific Variation of Viburnum Endocarps—We found relatively little variation within the four species sampled (Fig. S1). However, our samples of *V. dentatum* did show differences on the ventral and dorsal sides of the endocarp due to irregularities associated with grooving (Fig. S1).

Diversity of Viburnum Endocarps—We examined the distribution of endocarp form across *Viburnum* by plotting endocarp length against the ratio of width to perceived height (W:PH; Fig. 2). This showed that endocarp length varied widely within clades, but that most clades fell into clusters along the W:PH axis (Fig. 2). First, Oreinodentinus (Oreinotinus + Dentata), Tinus, *V. clemensiae*, and many species of Solenotinus have more or less spherical endocarp shapes in cross section (W:PH = 1–1.5), with little to no dorsal-ventral compression. At the other end of the W:PH spectrum are most species of Lentago, Lobata, Opulus, Punctata, and Urceolata, with distinctly flattened endocarps in cross section (W:PH of 2.5–4). The region in between these two extremes (W:PH of 1.5–2.5) contains the remaining *Viburnum* clades. Endocarps in this zone generally show some degree of dorsal-ventral compression with usually two dorsal and three ventral undulations roughly forming the shape of a "bat-silhouette." Although most clades are mainly confined to one of these three W:PH zones, Solenotinus, Sambucina, and Lutescentia, are more diverse and span two or all three of the zones. We also noted the absence of species with endocarps that are round and long (upper left quadrant of the morphospace) or flattened and short (lower right quadrant) (Fig. 2).

The PCA of the elliptical Fourier analysis of endocarp shape recovered 49.5% of the variation in the first principal component (PC) and 21.5% of the variation in the PC2 (Fig. S2). The morphospace created by PC1 and PC2 reflects the degree of curvature of the lateral "arms" of the endocarp around a ventral groove along PC1 and the degree of compression of the endocarp along PC2. As PC1 increases, the lateral arms of the endocarp shift from being curved around the ventral groove (creating a horseshoe shape) to uncurved (lacking a ventral groove). As values for PC2 increase, endocarps shift from more compressed to rounded.

Endocarp volume ranged from 0.9 cm^3 to 2.65 cm^3 with a mean of 0.59 cm^3 ($\pm$ 0.39 cm^3) and a median of 0.51 cm^3 (Table S1). Although for most species we have made measurements of only one or two endocarps, we note that our findings are consistent with descriptions and measurements of endocarp/seed sizes in the literature (e.g. Kern 1951; Donoghue 1983b; Hara 1983; Jacobs et al. 2008; Yang and Malécot 2011). Not surprisingly, clades containing many species (and with many species in our sample) show the greatest variation in endocarp volume. Oreinotinus, with 22 species in our sample, has a median size of 0.43 cm^3, but endocarps in this clade range from 0.20–2.65 cm^3, a difference of some 13-fold. Likewise, Succotinus, with 19 species in our sample, has a median endocarp volume of 0.37 cm^3, but ranges from 0.09–1.10 cm^3, for a 12-fold difference.

Although endocarp volume does vary considerably within clades (Table S1), we also note that volume does still broadly reflect phylogenetic relationships (Figs. S3, S4). We are struck, for example, that the Laminotinus clade has generally small endocarp volumes, with median values of 0.37 cm^3 in Succotinus, 0.35 cm^3 in Lobata, and 0.36 cm^3 in Coriacea. This contrasts with generally larger volumes in Valvatotinus, with median values of 0.78 cm^3 in Punctata, 0.77 cm^3 in Lentago, and 0.66 cm^3 in Euviburnum. Oreinodentinus shows intermediate values, with median values of 0.50 cm^3 in Dentata and 0.43 cm^3 in Oreinotinus.

Evolution of Viburnum Endocarps—The *Viburnum* phylogeny recovered here from our cpDNA + nrITS dataset is congruent with prior analyses based on these data (Fig. 3). Using this tree as well as the RAD-seq tree, we conducted ancestral character state analyses of W:PH, as this was the variable that best separated endocarp shapes (Fig. 3; Fig. S5). In the cpDNA + nrITS tree, the ancestor of Regulaviburnum was inferred to have had somewhat compressed endocarps with dorsal and ventral grooving (green in Fig. 3). Shifts to rounder endocarps (red and orange in Fig. 3) were seen in *V. clemensiae* and several clades (Tinus, Oreinotinus, and Solenotinus), while shifts to highly compressed endocarps (blue in Fig. 3) were especially evident in Opulus and Lentago. These derivative shapes also greatly reduce or lose the dorsal and ventral grooving. Despite topological differences in the RAD-seq tree, shifts from compressed endocarps with grooving to rounder and to highly compressed endocarps without grooving were identified in the same clades (Fig. S5).

Visualizing the tree in the morphospace (Fig. 4) confirmed that the majority of *Viburnum* clades occupied a part of the morphospace represented by the symplesiomorphic moderately compressed and grooved endocarp form. From there, several lineages independently explored different pathways to the round condition (lower PC1 scores) while also obtaining a wide range of lengths (PC2 in Fig. 4). On the PC2 axis, increasing PC2 scores included endocarps that appeared roughly round in cross section but had a large ventral intrusion or groove, with downward curving lateral arms. The PCA (Fig. 4; Fig. S2) did not as strongly separate highly compressed endocarps (in the upper right quadrant) with greatly reduced grooving as compared to other data visualization approaches (Figs. 2, 3).

Taken together, these analyses identified three instances of parallel evolution (Figs. 3, 4), which we further investigated using a statistical approach (Table 1; Fig. 5). The first major case of parallel evolution was of round shapes with limited grooving and little central intrusion, as seen in the Oreinotinus species of South America as well as Tinus and *V. clemensiae*. These species shared a low W:PH ratio (Fig. 2) and occupied an area of the phylomorphospace that was distinct from that of the ancestral endocarp shape (Fig. 4). To visualize the C1 calculation, we traced the branches leading to *V. tinus* L. (Tinus) and to *V. tinoides* L.f. (Oreinotinus) from their most recent common ancestor to the modern shapes through the morphospace to highlight maximum (D_{max}) and contemporary (D_{tip})

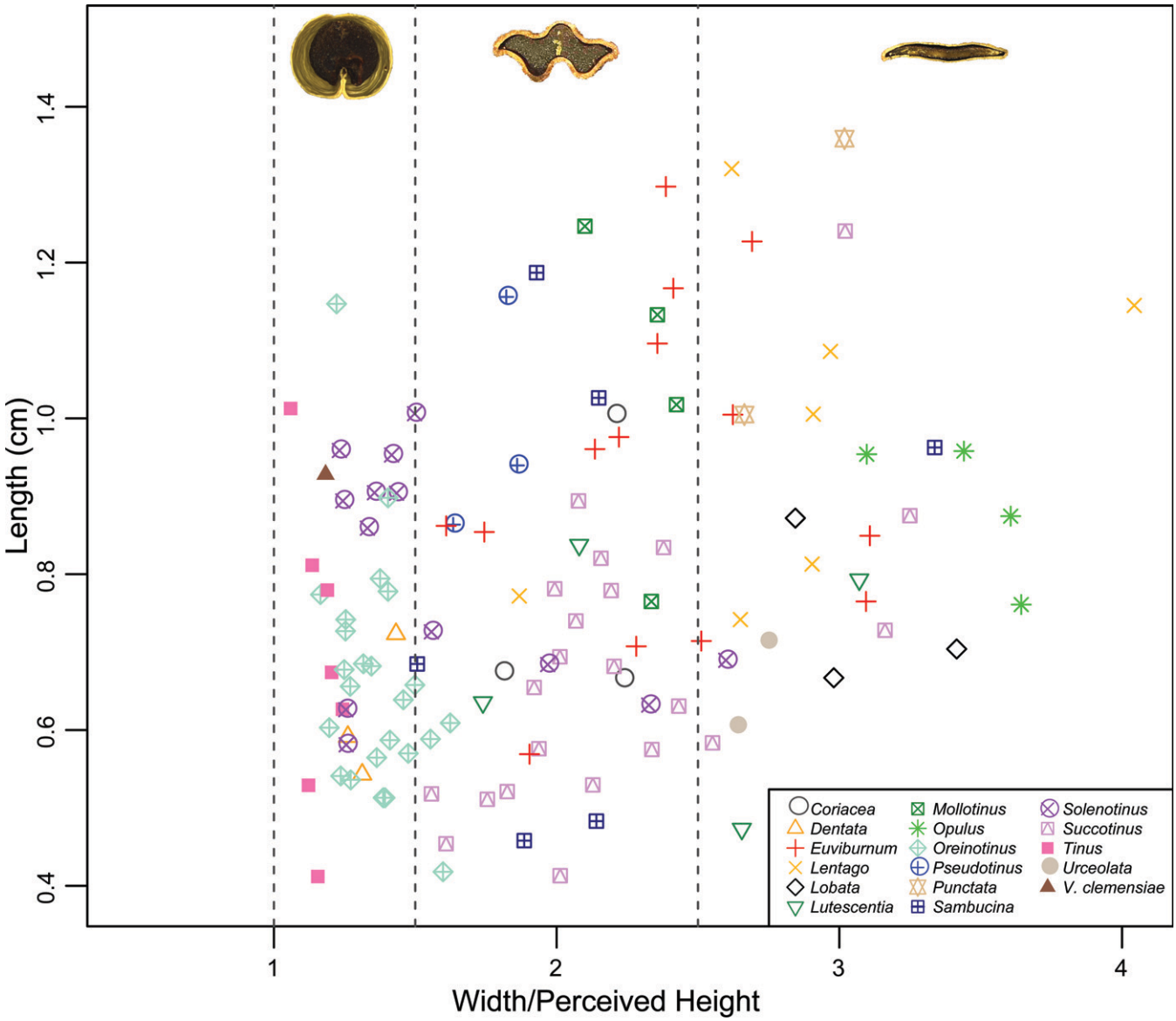

FIG. 2. Scatterplot showing the width/perceived height ratio on the X axis and absolute length on the Y axis (n = 122). Clades are denoted by color and symbol. Exemplar endocarps along the top show how an increase in the W:PH ratio corresponds to dorsal-ventral compression. Vertical dotted lines demarcate three regions of the morphospace that broadly correspond with endocarp form. Note that while lengths are variable within clades, Tinus, Oreinotinus, Dentata, Solenotinus, and *V. clemensiae* generally fall below a W:PH of 1.5, whereas Lentago, Opulus, Punctata, and Lobata fall above 2.5.

phenotypic distances (Fig. 5). The C1 values for this comparison and the majority of comparisons among the species of Tinus, South American Oreinotinus, and *V. clemensiae* demonstrated that these endocarps had evolved to be more similar than would have been expected by chance ($p < 0.05$; Table 1; Fig. 5), supporting our hypothesis that this endocarp form evolved in parallel in these three groups.

While Tinus, some Oreinotinus, and *V. clemensiae* have round endocarps virtually lacking a ventral intrusion (low PC1 and PC2 values; Fig. 4), most Solenotinus species are round in cross section but with a prominent ventral intrusion. Similar forms exist among the variable round endocarps of Oreinodentinus (Fig. 3). In particular, Dentata species have endocarps with a conspicuous ventral intrusion as do species of Oreinotinus from northern Mexico. We focused our statistical comparisons on *V. foetens* Decne. (Solenotinus), *V. dentatum* (Dentata), *V. loeseneri* Graebn., and *V. microcarpum* Schltdl. & Cham. (Oreinotinus species of northern Mexico). All of these comparisons yield significant C1 values ($p < 0.05$; Table 1; Fig. 5). Additional comparisons of species of Solenotinus, Dentata, and Mexican Oreinotinus species resulted in about half of these comparisons yielding significant C1 values ($p < 0.05$; Table 1; Fig. 5). These results support our hypothesis that rounded endocarps with a central intrusion have evolved in parallel in these clades.

The final endocarp form hypothesized to have evolved in parallel was compressed endocarps with little or no grooving, primarily observed in the Opulus and Lentago clades. We focused on comparing *V. lentago* L. (Lentago) and three species of the Opulus clade (*V. edule* (Michx.) Raf., *V. opulus* L., and *V. trilobum* Marshall), all of which yielded significant C1 values ($p < 0.05$; Table 1; Fig. 5). Nearly half of the comparisons between species of the Lentago and Opulus clades were more similar than expected by chance ($p < 0.05$; Table 1; Fig. 5). Additionally, species in two other clades, *V. schensianum* Maxim. of Euviburnum and *V. chingii* P.S.Hsu of Solenotinus, were seen to occupy the same region of the phylomorphospace as the

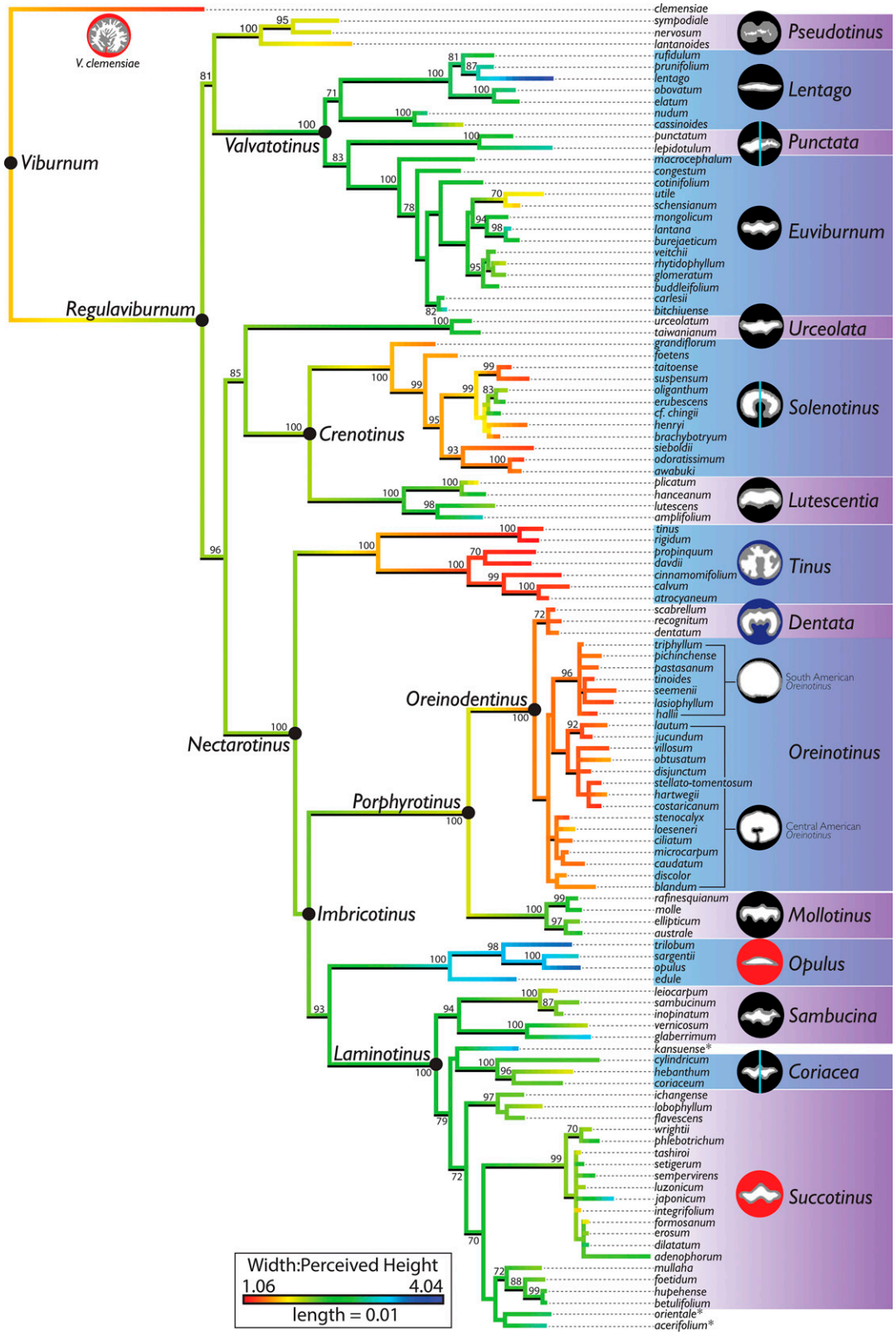

FIG. 3. Maximum clade credibility tree from the Bayesian analysis of cpDNA + nrITS data for 115 species of *Viburnum*, showing inferred ancestral Width:Perceived Height (W:PH) values. Posterior probabilities > 0.95 are indicated by black lines subtending branches and maximum likelihood bootstrap values > 70 are placed above or below the branches. Named clades of *Viburnum* (Clement et al. 2014) are indicated with a black dot adjacent to a node or to the right of the taxon names; members of Lobata (a clade recovered in RAD-seq analyses: Landis et al. 2020) do not form a clade here and are marked with an asterisk. Fruit cross sections for the named clades reflect the fruit and endocarp characters indicative of that group. Fruit cross sections show fruit color, endocarp shape, the relative amount of pulp, and ruminate endosperm. For clades with more than one endocarp form, either two separate fruit cross sections are shown (e.g. Oreinotinus), or a single cross section is shown with a blue line separating the two possible endocarp shapes on the left and right-hand sides of the fruit (e.g. Punctata, Solenotinus, and Coriacea).

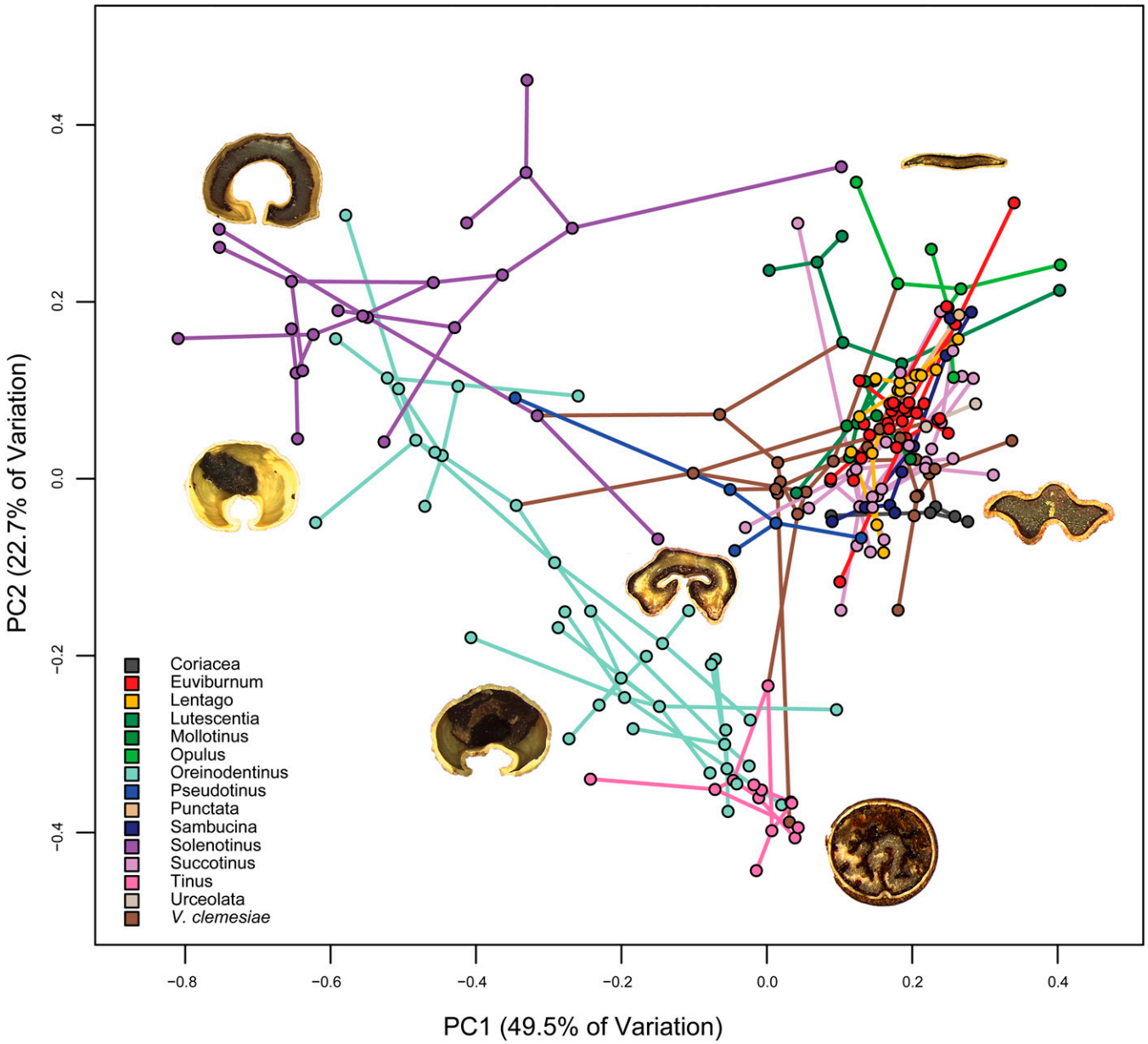

FIG. 4. Phylomorphospace based on the first two principal components from the Elliptical Fourier Analysis, showing *Viburnum* phylogeny based on nine plastid gene regions and nrITS (n = 115). Colors of the branches denote major *Viburnum* clades (Fig. 3). Representative endocarp images have been positioned to illustrate how shape varies across the morphospace.

majority of Opulus and Lentago species (Fig. 4). These species were also supported as having evolved this endocarp shape in parallel ($p < 0.05$; Table 1; Fig. 5).

DISCUSSION

Endocarp Morphology and Taxonomy—Endocarp shape has long been considered a diagnostic feature within *Viburnum* and is especially useful in distinguishing the traditional sections from one another (Oersted 1861; Rehder 1940; Hara 1983). Our analyses confirm that most of the major clades are distinguishable on this basis (Figs. 2, 4, 6). For instance, all species of the *Tinus* clade have rounded endocarps with a highly reduced ventral intrusion in cross section (Fig. 6D), while species of the Lentago clade have highly compressed endocarps with little grooving (Fig. 6A). Our analyses also recover distinctive shapes for several clades that have only recently been recognized; for example, the Punctata, Lutescentia, Sambucina, and Coriacea clades of the former *Viburnum* section *Megalotinus* (Maxim.) Rehder (Clement and Donoghue 2011; Clement et al. 2014; Figs. 3, 6A).

Importantly, characteristic endocarp shapes have been retained within the major clades despite considerable variation in endocarp/seed size within these clades (Fig. 2; Table S1; Figs. S3, S4). In addition to the broad phylogenetic patterns in endocarp volume highlighted above, we note that there are evolutionary patterns in endocarp size within some clades. In Oreinotinus, the aptly named *V. microcarpum* has an endocarp volume of 0.21 cm^3, and similarly small sizes are found in its eastern and central Mexican relatives (e.g. *V. caudatum* Greenm., 0.23 cm^3; *V. loeseneri*, 0.32 cm^3). In contrast, the nine species in our sample of the South American Oreinotinus clade

TABLE 1. Measurements of convergence following Stayton (2015). Categories of endocarp shape hypothesized to have evolved in parallel include round endocarps with and without a central intrusion and compressed endocarps without grooving. For each comparison of a pair of species, C1 and a corresponding *p* value are reported. For clade-level comparisons, average C1 and *p* values are reported, representing all possible pairwise species comparisons between clades. Additionally, we report the proportion of such pairwise comparisons that are significant. Northern Mexican Oreinotinus are *V. caudatum*, *V. ciliatum*, *V. loeseneri*, *V. microcarpum*, and *V. stenocalyx*. Figure 5 shows the location in the phylomorphospace of the species and clades examined here.

	C1	*p*	Proportion significant
Round without central intrusion			
V. clemensiae + *V. tinus*	0.9638	0.0000	–
V. clemensiae + Tinus	0.8826	0.0198	6/7
V. clemensiae + *V. tinoides*	0.8635	0.0000	–
V. clemensiae + S.A. Oreinotinus	0.7620	0.0156	7/7
V. tinus + *V. tinoides*	0.8266	0.0000	–
Tinus + S.A. Oreinotinus	0.7490	0.0337	35/49
Round with central intrusion			
V. dentatum + *V. microcarpum*	0.7195	0.0396	–
V. dentatum + *V. loeseneri*	0.5713	0.0594	–
Dentata + N. Mexican Oreinotinus	0.6919	0.0462	8/15
V. foetens + *V. microcarpum*	0.7060	0.0396	–
V. foetens + *V. loeseneri*	0.7463	0.0396	–
Solenotinus + N. Mexican Oreinotinus	0.5834	0.1616	30/60
V. dentatum + *V. foetens*	0.4577	0.1188	–
Dentata + Solenotinus	0.5984	0.1356	18/36
Compressed without grooving			
V. opulus + *V. lentago*	0.6840	0.0297	–
V. trilobum + *V. lentago*	0.7572	0.0297	–
V. edule + *V. lentago*	0.2326	0.3465	–
Opulus + Lentago	0.5850	0.0902	13/28
V. schensianum + *V. opulus*	0.8394	0.0000	–
V. schensianum + *V. lentago*	0.7718	0.0198	–
V. schensianum + *V. chingii*	0.7042	0.0198	–
V. chingii + *V. opulus*	0.8119	0.0198	–
V. chingii + *V. lentago*	0.6784	0.0198	–

have much larger endocarps, averaging 0.81 cm^3. This difference in overall endocarp volume corresponds with a change in shape. As Oreinotinus spread from North to South America (Landis et al. 2020), the ventral intrusion was reduced. Other noteworthy cases of endocarp size variation within clades include the relatively large sizes of the Chinese *V. setigerum* Hance (1.10 cm^3) and its Japanese sister species, *V. phlebotrichum* Siebold & Zucc. (0.63 cm^3) within Succotinus (where the median endocarp volume is 0.37 cm^3). In the Lentago clade, *V. cassinoides* L. (0.34 cm^3) and *V. nudum* L. (0.42 cm^3) have much smaller endocarps than members of their sister clade, especially *V. rufidulum* Raf. (1.35 cm^3) and *V. prunifolium* (1.37 cm^3).

Parallel Evolution of Viburnum Fruit Syndromes—Beyond confirming the taxonomic value of sometimes rather subtle differences in endocarp shape, our phylogenetic analyses allowed us to trace the paths of endocarp evolution. We examined such patterns using two tree topologies, the first based on cpDNA + nrITS data (Fig. 3) and the second based largely on RAD-seq data (Landis et al. 2020; Fig. S5). We have featured the cpDNA + nrITS tree in Fig. 3 in order to highlight our latest analysis of this expanding dataset, but all of our basic conclusions regarding the evolution of endocarp shapes are supported on both trees (see below and Fig. S5).

The endocarps of the first viburnums were likely moderately compressed, with two shallow dorsal grooves and three shallow ventral grooves (cf. Jacobs et al. 2008). Endocarps of this form are featured in Fig. 6A, with arrows marking the grooves as seen in a cross section of *V. buddleifolium* C.H.Wright of the Euviburnum clade. This basic form was retained in multiple clades, though with slight but consistent differences in shape and size (Fig. 6A). From this starting point there appear to have been several parallel shifts in endocarp form. Highly

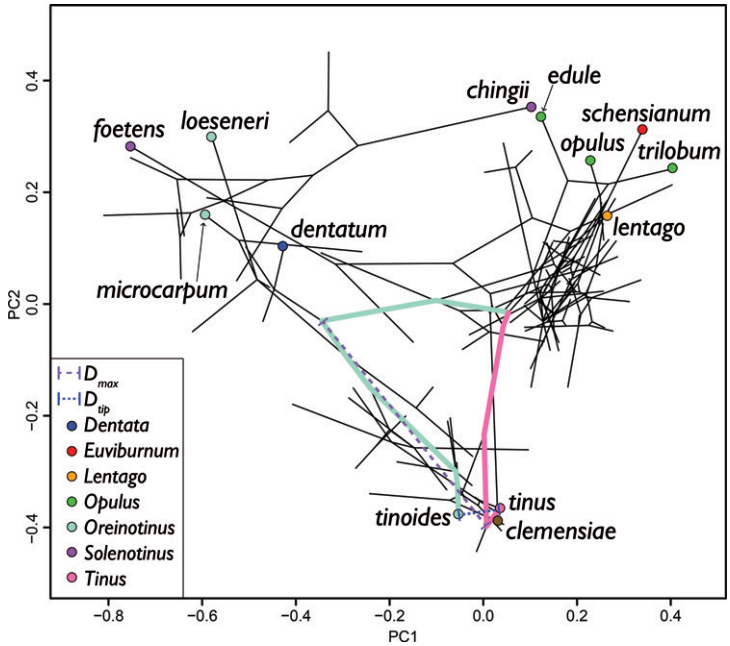

FIG. 5. Phylomorphospace highlighting species used in calculating C1 values and statistical significance (Stayton 2015). Highlighted are the branches connecting two focal taxa, *V. tinoides* (Oreinotinus) and *V. tinus* (Tinus), that independently evolved round endocarps without a central intrusion independently. D_{max} is the maximum Euclidian distance (dashed line) separating the branches leading to *V. tinoides* from the branches leading to *V. tinus*; D_{tip} is the Euclidean distances (dotted line) between the modern endocarp forms of *V. tinoides* and *V. tinus*. For any two species being compared, C1 = 1- (D_{tip}/D_{max}). All taxa highlighted in pairwise species comparisons in Table 1 are labeled and colored by clade.

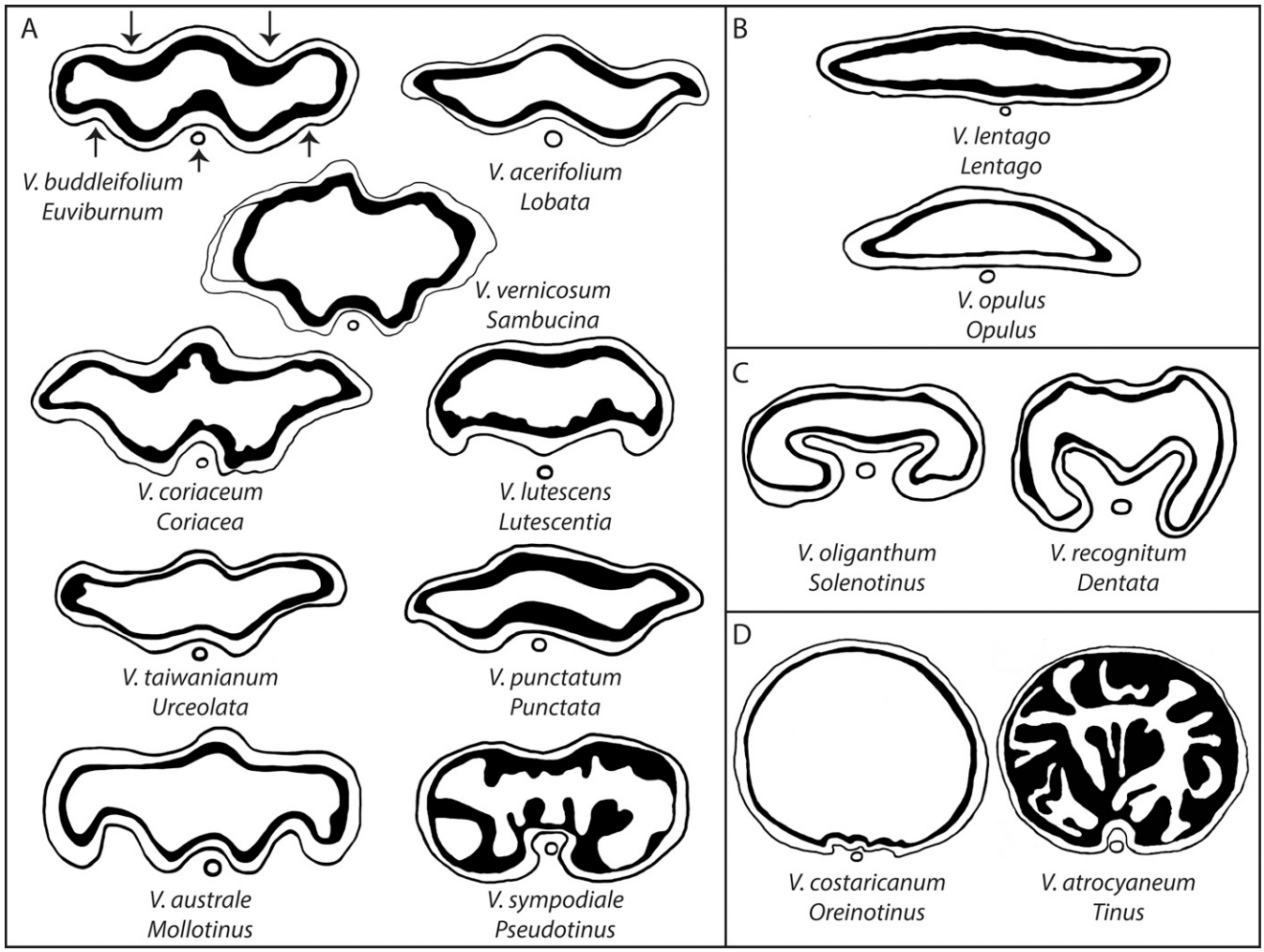

FIG. 6. Representative endocarp shapes for each major *Viburnum* clade. Endocarp cross sections are from camera lucida drawings of endocarps obtained from herbarium specimens. The outermost white area represents the endocarp and the inner black area represents the seed coat (testa). The black seed coat can be variously thickened (e.g. *V. lutescens*) or show more complex patterns of rumination extending into the endosperm (e.g. *V. atrocyaneum*). The small circle underneath each endocarp form represents the central vascular bundle that runs along the ventral axis of the ovary. A. Endocarp shapes more or less corresponding with an inferred ancestral endocarp that is compressed and grooved. Arrows associated with *V. buddleifolium* indicate the two dorsal and three ventral grooves characteristic of this ancestral endocarp form. B–D. Derived endocarp forms. B. Parallel evolution of compressed endocarps without grooving. C. Parallel evolution of round endocarps with a central intrusion. D. Parallel evolution of round endocarps with a very reduced central intrusion.

compressed and more or less grooveless endocarps evolved independently, most notably in the *Opulus* and Lentago clades (Fig. 6B). Rounded endocarps evolved separately in the Tinus and Oreinodentinus clades, in some members of the Solenotinus clade, and in *V. clemensiae*. More specifically, rounded but horseshoe-shaped endocarps (i.e. with a prominent ventral intrusion), characterize the Dentata clade in eastern North America, several species of Oreinotinus in northern Mexico, and some Solenotinus in Asia (Fig. 6C). The ventral groove is almost completely absent in Tinus species in Eurasia, in the species of Oreinotinus from southern Mexico to South America, and in *V. clemensiae* of Borneo (Fig. 6D). These changes appear to have been unidirectional; that is, we have inferred no reversals from the several derived endocarp forms back to a more ancestral form.

We are also able to assess how changes in endocarp shape have been related to changes in other fruit traits: color development pattern (sequential versus synchronous, Fig. 1F–G), mature fruit color, and, for some species, the volume, moisture, lipid, and sugar content of the mesocarp (Sinnott-Armstrong et al. 2020). Sinnott-Armstrong et al. (2020) focused special attention on two derived "fruit syndromes" within *Viburnum*, both of which evolved several times. In one of these syndromes, flattened endocarps are associated with red color, and with ample watery mesocarp tissue, rich in carbohydrates. In the other, rounded endocarps are associated with blue color, and with a thin mealy-textured mesocarp, rich in lipids. Our results are fully consistent with the recognition of these two syndromes, but here we recognize other trait combinations that involve fewer fruit variables and occur only occasionally. Such combinations of traits have arisen in several different ways. In some cases, the inferred ancestral endocarp shape has been retained in a lineage that has subsequently evolved a different color, mesocarp type, and/or nutritional content. For example, Mollotinus species appear to have maintained the ancestral endocarp shape (Figs. 3, 4, 6A), but they differ from inferred ancestral fruits in undergoing synchronous color development and in having higher lipid content (Sinnott-Armstrong et al. 2020). Other combinations have come about as endocarp shape has evolved within clades that have otherwise

retained ancestral fruit traits. For example, species in the Solenotinus clade appear to have retained sequential color maturation, intermediate pulp volume, and low lipid content, yet within this clade a number of different endocarp shapes have evolved, including derived horseshoe-shaped forms (Figs. 3, 4, 6C).

In yet other cases, several fruit traits appear to have evolved along the same branch in the tree, and this has yielded several evolutionarily one-off fruit types. The best example is *V. clemensiae*. Although some uncertainty remains about the exact phylogenetic placement of this species (Landis et al. 2020), it is clear that it represents a very early and long branch in the *Viburnum* tree. It appears to have evolved a rounded endocarp, but with red color at maturity, a reduced mealy mesocarp, and a peculiar form of ruminate endosperm (Jacobs et al. 2008; Clement et al. 2014). As this combination evolved nowhere else in *Viburnum*, it was not flagged as a syndrome by Sinnott-Armstrong et al. (2020). But, cases like this show us that elements of the syndromes of Sinnott-Armstrong et al. (2020) do not strictly co-occur. Round endocarps are associated with several other traits in the blue syndrome of Sinnott-Armstrong et al. (2020), and, likewise, flattened endocarps are characteristic of the red syndrome. However, these derived endocarp shapes are not limited to these two syndromes. In fact, some of the most extreme cases of parallel evolution of a particular derived endocarp shape (Fig. 5; Table 1) appear in the context of otherwise highly divergent fruits. An excellent example of such parallelism is the evolution of similar rounded endocarps in *V. clemensiae* on the one hand, and in the Tinus clade on the other hand. The same is also true of highly flattened endocarps. These are found in the Opulus clade, in which the fruits are red and juicy (hence the red syndrome), but they also evolved in the Lentago clade in the context of sequential color development, black color at maturity, and mealy texture.

On the Evolution of 'Fruit Syndromes'—What do these observations tell us about fruit evolution? The appearance of very similar endocarp shapes in different fruit backgrounds assures us that these traits can indeed evolve independently of one another. It also shows that there is a wider range of functional configurations than the several syndromes recognized by Sinnott-Armstrong et al. (2020) may suggest. The one-off fruits of *V. clemensiae* demonstrate that round endocarps need not be associated with the blue syndrome, and, therefore, that there are likely other factors driving endocarp shape. What these factors are is unclear. A particular endocarp shape may evolve to maximize dispersal by particular resident or migratory birds, but endocarp shape relates to other functions such as seed germination, and the combinations of fruit traits that we observe presumably represent trade-offs with respect to these various functions. Such trade-offs extend to other features that we have not focused on here, perhaps especially seed coat traits, including the production of ruminate endosperm in a number of clades. Notably, although the round endocarps of Tinus, Oreinotinus, and *V. clemensiae* have evolved in parallel, they have diverged significantly in several other seed traits (Jacobs et al. 2008). Tinus and *V. clemensiae* have well-developed ruminate endosperm, but of different developmental types (Type 2A in *V. clemensiae* and Type 2B in Tinus; Jacobs et al. 2008), whereas ruminate endosperm is absent or very limited in Oreinotinus (Fig. 6D). Likewise, there are marked differences in endocarp and seed coat thickness and cell structure, some of which are highly consistent with phylogeny. For example, thinner seed coats of cuboidal or rectangular cells appear to mark the entire Nectarotinus clade, while the rest of the species have retained a thicker testa with palisade-shaped cells (cf. Jacobs et al. 2008).

Even more generally, how do these observations bear on the concept of syndromes? In reflecting on fruit syndromes, a comparison to the familiar pollination syndromes is useful. We recognize a certain combination of flower traits as the hummingbird pollination syndrome: long tubular red-colored corollas that open during the day and produce copious nectar and little scent. This combination has emerged repeatedly, in distantly related angiosperm lineages in relation to selection by hummingbirds, with their particular perceptual abilities (e.g. Abrahamczyk and Renner 2015). But, it is clear that the individual elements of the hummingbird syndrome have evolved elsewhere, sometimes in relation to other pollinators. For example, long tubular corollas have also evolved in connection with hawkmoth pollination, where the flowers are typically white, scented, and open at night. Observations such as this do not diminish the value of recognizing syndromes, but they do serve to highlight that particular traits of interest can evolve independently of the traits with which they are most often associated, and that they can potentially function in connection with multiple syndromes or fall completely outside of commonly described syndromes (Ollerton et al. 2009; Rosas-Guerrero et al. 2014). They also highlight that a given trait can influence a variety of functions at once. A long corolla tube might attract particular pollinators, but could also keep out unwanted visitors. Nevertheless, it is important to note that particular traits, such as tubular corollas, do not evolve in connection with every pollination syndrome (e.g. with beetle or wind pollination).

All of these observations apply to the traits that constitute fruit syndromes, and we note, in particular, that not all species fall within proposed syndromes, nor do we observe every possible combination of fruit traits in *Viburnum* or more generally (cf. Beaulieu and Donoghue 2013). For example, we do not find flattened endocarps with scant lipid-rich flesh and blue color, or round endocarps embedded in a copious watery mesocarp. This implies that such combinations are either not evolutionarily accessible, or that they have not evolved because they would function poorly. Compared to the traits associated with pollination syndromes, we still know very little about the function of most fruit traits (except in the broadest terms; e.g. fleshy fruits are selected by birds). Nevertheless, speculation on function can be useful in framing potential tests. For example, we might hypothesize that large endocarps surrounded by a thin layer of watery mesocarp are not found because in order for birds to assume the costs associated with ingesting a large endocarp, fruits need to provide sufficient nutritional benefit; for example, by providing either a large amount of flesh or flesh rich in lipids.

Conclusions

The colorful drupe fruits of *Viburnum* hide a wide array of endocarp shapes within. The sometimes subtle variation in endocarp shape can be difficult to describe, but our morphometric and phylogenetic analyses demonstrate that endocarp shapes are largely consistent within and among species. Also, different shapes distinguish many of the major clades within *Viburnum* despite considerable variation in absolute size. Our quantitative analyses provide statistical support for several cases of parallel evolution from a moderately flattened and

grooved ancestral form toward rounded forms and ungrooved flattened forms. In some cases, these shifts are tightly correlated with changes in the color and nutritional content of the pulp, which supports the recognition of derived fruit "syndromes" that have evolved several times independently and may relate to dispersal primarily by resident versus migrant birds (Sinnott-Armstrong et al. 2020). However, our expanded analyses, focused specifically on endocarp form, highlight that parallel evolution in endocarp shape sometimes occurs in drupes that are otherwise highly dissimilar. While this confirms that these fruit traits can vary quite independently, it also demonstrates the existence of an even wider variety of strategies with respect to dispersal and/or germination. Our results set the stage for understanding the integrated evolution of an entire set of fruit and seed traits in relation to the several vital functions that they carry out.

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Author Contributions

WLC and MJD designed the research project, AG and PG collected sequence data and conducted phylogenetic analyses, TJS photographed and collected endocarp morphology data, TJS and WLC conducted analyses, and WLC and MJD drafted the paper.

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APPENDIX 1. Voucher information and GenBank accession numbers for all plant material used in phylogenetic analyses and studies of endocarp morphology. Species are arranged alphabetically and missing data are indicated with a dash (–). For each species, the following information is provided: *voucher specimen for molecular work*, herbarium, GenBank accession numbers for *matK*, *ndhF*, *petB-petD*, *rbcL*, *rpl*32-*trnL*$^{(UAG)}$, *trnC-ycf6*, *trnH-psbA*, *trnK*, *trnS-trnG*, ITS; *voucher specimen for morphological work*, herbarium, specimen type (CL = camera lucida drawing; H = herbarium; P = pickled). Herbarium abbreviations follow Index Herbariorum (Thiers 2020) and NVI refers to no voucher information.

V. acerifolium L., *M.J. Donoghue & R.C. Winkworth 27*, YU, HQ591557, HQ591641, HQ591987, HQ591701, HQ591863, HQ592108, AY627384, AY265160, HQ591819, AY265114; *C.G. Pringle 207*, A, H. ***V. adenophorum*** W.W.Smith, *D.E. Boufford & B. Bartholomew 24402*, A, HQ591558, –, HQ591988, HQ591702, HQ591864, HQ592109, HQ592057, HQ591781, MT025847, HQ591948; *D.E. Boufford & B. Bartholomew 24803*, A, H. ***V. amplifolium*** Rehder, *P.W. Sweeney et al. 2252*, YU, MN914753, MN937378, MN987749, MN937409, MN987905, MN987683, MN987817, MN987865, MN987633, MN952543; *H.T. Tsai 61436*, A, CL. ***V. atrocyaneum*** C.B.Clarke, *D.E. Boufford et al. 34956*, A, HQ591559, HQ591642, HQ591989, HQ591703, HQ591866, HQ592110, HQ592059, HQ591782, HQ591820, HQ591950; *K.M. Feng 3054*, A, CL. ***V. australe*** Morton, *M.A. Carranza et al. 2064*, MO, JQ805235, –, –, JQ805393, –, KP281879, JQ805304, KP281896, –, JQ805157; *M.J. Donoghue 2*, YU, H. ***V. awabuki*** K.Koch, *S.-M. Liu et al. 141*, A, HQ591560, –, HQ591990, HQ591704, HQ591867, HQ592111, HQ592060, HQ591783, –, HQ591951; *Walker et al 6058*, A, CL. ***V. betulifolium*** Batalin, *P.W. Sweeney et al. 2344*, YU, MN914760, MN937385, MN987756, MN937416, MN987912, MN987690, MN987824, MN987872, MN987640, MN952550; *B. Bartholomew et al. 1415*, A, CL. ***V. bitchiuense*** Makino, *D. Chatelet 1097-77A*, *Arnold Arboretum living collection*, JX049451, JX049459, JX049509, JX049471, JX049477, JX049481, JX049467, JX049491, JX049495, JX049448; *NVI*, CL. ***V. blandum*** C.V.Morton, *M.J. Donoghue 464*, YU, HQ591562, –, HQ591992, HQ591706, HQ591869, HQ592113, HQ592062, HQ591785, –, HQ591952; *M.J. Donoghue 339*, YU, H. ***V. brachybotryum*** Hemsl. Et F.B.Forbes & Hemsl., *P.W. Sweeney et al. 2222*, YU, MN914761, MN937386, MN987757, MN937417, MN987913, MN987691, MN987825, –, MN987641, MN952551; *E.H. Wilson 1840*, A, CL. ***V. buddleifolium*** C.H.Wright, *P.W. Sweeney et al. 2607*, YU, MN914762, MN937387, MN987758, MN937418, MN987914, MN987692, MN987826, MN987873, MN987642, MN952552; *E.H. Wilson 1838*, A, CL. ***V. burejaeticum*** Regel & Herder, *K. Schmandt 375-95A*/00223095, A, JQ805231, JX049463, JX049513, JX049463, JX049473, JQ805472, JX049486, JQ805297, JQ805552, JX049500, –; *P.H. Dorsett 4204*, A, CL. ***V. calvum*** Rehder, *H. Li & V. Soukup 934*, A, HQ591565, HQ591644, HQ591995, HQ591709, HQ591872, HQ592116, HQ592066, HQ591788, JX049508, HQ591955; *H.T. Tsai 52358*, A, CL. ***V. carlesii*** Hemsl. ex Forb. & Hemsl., *M.J. Donoghue & R.C. Winkworth 24*, YU, HQ591566, HQ591645, HQ591996, HQ591710, HQ591873, HQ592117, AY627385, AY265161, HQ591823, AY265115; *E.H. Wilson 10601*, A, CL. ***V. cassinoides*** L., *E.L. Spriggs 79*, YU, MN914763, MN937388, MN987759, MN937419, MN987915, MN987693, MN987827, –, MN987643, MN952553; *ELS 232* YU, *E.L. Spriggs 408* A, H. ***V. caudatum*** Greenm., *M.J. Donoghue 64*, YU, –, –, –, –, HQ591875, HQ592119, HQ592068, HQ591790, HQ591825, HQ591957; *M.J. Donoghue 38*, YU, H. ***V. chingii*** P.S.Hsu, *P.W. Sweeney et al. 2247*, YU, MN914764, MN937389, MN987760, MN937420, MN987916, MN987694, MN987828, MN987874, MN987644, MN952554; *B. Bartholomew et al. 1379*, A, CL. ***V. ciliatum*** Greenm., *M.J. Donoghue 48*, YU, JQ805240, –, MT025838, JQ805401, MT025851, MT025841, JQ805311, JQ805563, –, –; *NVI*, CL. ***V. cinnamomifolium*** Rehder, *P.W. Sweeney et al. 2255*, YU, MN914765, MN937390, MN987761, MN937421, MN987917, MN987695, MN987829, MN987875, MN987645, MN952555; *NVI*, CL. ***V. clemensiae*** Kern, *J. Beaman 11781*, K, HQ591569, HQ591648, HQ591999, HQ591714, HQ591878, HQ592122, AY627387, AY265163, EF490267, AY265117; *P.W. Sweeney et al. 2145*, YU, H. ***V. congestum*** Rehder, *P.W. Sweeney et al. 2235*, YU, MN914754, MN937379, MN987750, MN937410, MN987906, MN987684, MN987818, MN987866, MN987634, MN952544; *P.W. Bristol 42*, A, CL. ***V. coriaceum*** Bl., *P.W. Sweeney et al. 2088*, YU, KP281810, KP281828, KP281864, KP281818, KP281854, KP281876, KP281845, KP281893, KP281902, KP281840; *M. Balgooy, K. W. Riadinata 2890*, A, H. ***V. costaricanum*** Hemsl., *M.J. Donoghue 85*, YU, –, KP281831, –, –, JQ805482, –, –, JQ805564, KF019909, JQ805164; *M.J. Donoghue 645*, YU, H. ***V. cotinifolium*** D.Don, *M.J. Donoghue WC267*, YU, KF019744, KF019767, KF019823, KF019787, KF019864, –, KF019843, KF019932, KF019908, KF019809; *R.R. Stewart 17253*, A, CL. ***V. cylindricum*** Buch.-Ham. ex D.Don, *P.W. Sweeney et al. 2233*, YU, MN914766, MN937391, MN987762, MN937422, MN987918, MN987696, MN987830, MN987876, MN987646, MN952556; *H.T. Tsai 59828*, A, CL. ***V. davidii*** Franch., *M.J. Donoghue WC269*, YU, KF019765, KF019785, KF019841, KF019807, KF019883, KF019906, KF019862, KF019951, KF019930, KF019821; *E.H. Wilson 963*, A, CL. ***V. dentatum*** L., *M.J. Donoghue & R.C. Winkworth 33*, YU, HQ591574, HQ591651, HQ592002, HQ591718, HQ591884, HQ592128, AY627391, AY265167, HQ591827, AY265121; *F.W. Hunnewell 4551*, GH, CL. ***V. dilatatum*** Thunb., *P.W. Sweeney et al. 2209*, YU, MN914767, MN937392, MN987763, MN937423, MN987919, MN987697, MN987831, –, MN987647, –; *I. Hurusawa 1418*, A, CL. ***V. discolor*** Benth., *M. Veliz, N. Gallardo, M. Vasquez 35-99*, MO, JQ805241, –, –, JQ805402, JQ805485, KF019886, JQ805314, MT025846, –, JQ805166; *M.J. Donoghue 507*, YU, CL. ***V. disjunctum*** C.V.Morton, *M.J. Donoghue 700*, YU, KF019745, –, –, KF019788, –, KF019887, KF019844, –, KF019910, KF019810; *M.J. Donoghue 492*, YU, H. ***V. edule*** (Michx.) Raf., NVI, HQ591577, –, –, HQ591720, –, –, AY627393, AY265169, EF490271, AY265123; *M.C. Fernald, L.B. Smith 26029*, GH, CL. ***V. elatum*** Benth., *P.W. Sweeney et al. 3063*, YU, MN914768, MN937393, MN987764, MN937424, MN987920, –, MN987832, –, MN987648, MN952557; *NVI*, CL. ***V. ellipticum*** Hook., *M.J. Donoghue NVI*, HQ591579, HQ591653, HQ592004, HQ591722, –, HQ592131, AY627395, AY265171, HQ591830, AY265125; *W.N. Suksdorf 6119*, A, CL. ***V. erosum*** Thunb., *M.J. Donoghue et al. 4*, YU, MN914769, MN937394, MN987765, MN937425, MN987921,

MN987698, MN987833, MN987877, MN987649, –; *M. Togasi 649, H. Muroi 6069*, A, CL. ***V. erubescens*** Wall., *Boufford et al. 27190*, A, HQ591581, HQ591655, HQ592006, HQ591724, HQ591889, HQ592133, AY627397, AY265173, HQ591831, AY265127; *J.F. Rock 6847, E.H. Wilson 305*, A, CL. ***V. flavescens*** W.W.Smith, *Boufford et al. 32758*, A, HQ591583, HQ591657, HQ592008, HQ591726, HQ591891, –, HQ592074, HQ591794, JX049505, HQ591962; *K.M. Feng 2921*, A, H. ***V. foetens*** Decne., *M.J. Donoghue WC270*, YU, KF019754, KF019774, KF019831, KF019796, KF019872, KF019895, KF019851, KF019940, KF019919, KF019813; *Shahzad et al 113*, A, CL. ***V. foetidum*** Wall., *M.J. Donoghue & K-F. Chung KFC1942*, YU, KF019759, KF019779, KF019835, KF019801, KF019877, KF019900, KF019856, KF019945, KF019924, KF019818; *H.F. Handel-Mazzetti 771*, A, CL. ***V. fordiae*** Hance, no molecular data; *W.Y. Chun 5224*, A, CL. ***V. formosanum*** Hayata, *M.J. Donoghue & J.M. Hu J-M Hu 2007*, YU, KF019760, KF019780, KF019836, KF019802, KF019878, KF019901, KF019857, KF019946, KF019925, –; *B. Bartholomew et al. 434* A, H. ***V. glaberrimum*** Merr., *P.W. Sweeney et al. 2322*, YU, MN914755, MN937380, MN987751, MN937411, MN987907, MN987685, MN987819, MN987867, MN987635, MN952545; *M. Jacobs 7434*, A, CL. ***V. glomeratum*** Maxim., *P.W. Sweeney et al. 2559*, YU, MN914770, MN937395, MN987766, MN937426, MN987922, MN987699, MN987834, MN987878, MN987650, MN952558; *J. Hers 2782*, A, CL. ***V. grandiflorum*** Wall. ex DC, *M.J. Donoghue WC271*, YU, KF019755, KF019775, KF019832, KF019797, KF019873, KF019896, KF019852, KF019941, KF019920, KF019814; *S. Noshiro, N. Fujii, T Kajita, K Yoda 9480199*, A, H. ***V. hallii*** Killip & A.C.Smith, *P.W. Sweeney et al. 1626*, YU, JQ805248, –, MT025839, JQ805410, JQ805492, MT025842, JQ805322, JQ805572, MT025848, JQ805173; *P.W. Sweeney et al. 1825*, YU, H. ***V. hanceanum*** Maxim., *P.W. Sweeney et al. 2195*, YU, MN914756, MN937381, MN987752, MN937412, MN987908, MN987686, MN987820, MN987868, MN987636, MN952546; *W.Y. Chun 7173*, A, H. ***V. hartwegii*** Benth., *M.J. Donoghue 40*, YU, HQ591586, HQ591659, HQ592011, –, HQ591894, HQ592137, AY627400, AY265176, HQ591832, AY265130; *M.J. Donoghue 672*, YU, H. ***V. hebanthum*** Wight & Arn., *J. Klackenberg 32*, NY, HQ591587, HQ591660, HQ592012, HQ591729, HQ591895, HQ592138, HQ592076, HQ591795, HQ591833, –; *E.H. Wilson s.n.*, A, CL. ***V. henryi*** Hemsl., *M.J. Donoghue WC272*, YU, KF019756, KF019776, –, KF019798, KF019874, KF019897, KF019853, KF019942, KF019921, KF019815; *Fang 2473*, A, CL. ***V. hondurense*** Standl., no molecular data; *Lopez 67*, GH, H. ***V. hupehense*** Rehder, *Bartholomew et al. 1286*, A, HQ591588, HQ591661, HQ592013, HQ591730, HQ591896, HQ592139, HQ592077, HQ591796, HQ591834, HQ591964; *E.H. Wilson 237, 1025*, A, CL. ***V. ichangense*** Rehder, *Bartholomew et al. 1889*, A, HQ591589, HQ591662, HQ592014, HQ591731, HQ591897, HQ592140, HQ592078, HQ591797, HQ591835, HQ591965; *E.H. Wilson 221, B. Bartholomew et al. 446*, A, CL. ***V. inopinatum*** Craib., *P.W. Sweeney et al. 2091*, YU, KF019750, KF019770, KF019827, KF019792, KF019868, KF019891, KF019847, KF019936, KF019915, KJ795808; *J.F. Maxwell 89-1444*, A, H. ***V. integrifolium*** Hayata, *M.J. Donoghue & K-F. Chung KFC1946*, YU, KF019761, KF019781, KF019837, KF019803, KF019879, KF019902, KF019858, KF019947, KF019926, –; *K-F. Chung 1945*, YU, H. ***V. japonicum*** Spreng, *NVI*, YU, HQ591592, HQ591664, HQ592016, HQ591733, HQ591899, HQ592143, AY627401, AY265177, HQ591837, AY265131; *Maximowicz 1863*, A, CL. ***V. jucundum*** C.V.Morton, *M.J. Donoghue 244*, YU, HQ591593, HQ591665, HQ592017, HQ591734, HQ591900, –, AY627402, AY265178, HQ591838, AY265132; *M.J. Donoghue 309*, YU, H. ***V. kansuense*** Batalin, *Boufford et al. 27416*, A, HQ591594, HQ591666, HQ592018, HQ591735, HQ591901, HQ592144, AY627403, AY265179, EF490276, AY265133; *D.E. Boufford, M.J. Donoghue, R.H. Ree 27348*, A, H. ***V. lantana*** L., *M.J. Donoghue & R.C. Winkworth 26*, YU, HQ591595, HQ591667, HQ592019, HQ591736, HQ591902, HQ592145, AY627404, AY265180, EF490278, AY265134; *D.P. Nikolaev, T.N. Medvedev s.n.*, A, H. ***V. lantanoides*** Michx., *M.J. Donoghue & R.C. Winkworth 2*, YU, HQ591596, HQ591668, HQ592020, HQ591737, HQ591903, HQ592146, AY627405, AY265181, EF490279, AY265135; *S.H. Burnham s.n.*, GH, CL. ***V. lasiophyllum*** Benth., *P.W. Sweeney et al. 2174*, YU, KP281814, KP281834, KP281869, KP281822, KP281859, KP281884, KP281849, –, KP281907, –; *P.W. Sweeney et al. 2174*, YU. ***V. lautum*** C.V.Morton, *M.J. Donoghue 72*, YU, HQ591597, HQ591669, HQ592021, HQ591738, HQ591904, HQ592147, HQ592082, HQ591799, HQ591839, HQ591967; *M.J. Donoghue 103*, YU, H. ***V. leiocarpum*** P.S.Hsu, *P.W. Sweeney et al. 2265*, YU, MN914757, MN937382, MN987753, MN937413, MN987909, MN987687, MN987821, MN987869, MN987637, MN952547; *K.M. Feng 13870*, A, H. ***V. lentago*** L., *M.J. Donoghue & R.C. Winkworth 21*, YU, HQ591598, HQ591670, HQ592022, HQ591739, HQ591905, HQ592148, AY627406, AY265182, EF490280, AY265136; *Whetzel 12955* GH, H. ***V. lepidotulum*** Merr. & Chun, *P.W. Sweeney et al. 2097*, YU, KF019748, KF019768, KF019825, KF019790, KF019866, KF019889, –, KF019934, KF019913, KJ795805; *P.W. Sweeney et al. 2101*, YU, H. ***V. lobophyllum*** Graebn., *M.J. Donoghue & R.C. Winkworth 25*, YU, HQ591600, HQ591671, HQ592023, HQ591741, HQ591907, HQ592149, AY627407, AY265183, HQ591840, AY265137; *B. Bartholomew et al. 1416*, A, CL. ***V. loeseneri*** Graebn., *M.J. Donoghue 2547*, YU, HQ591601, –, HQ592024, HQ591742, HQ591908, HQ592150, HQ592084, HQ591801, –, HQ591968; *M.J. Donoghue 2547*, YU, H. ***V. lutescens*** Bl., *P.W. Sweeney et al. 2077*, YU, MN914771, MN937396, MN987767, MN937427, MN987923, MN987700, –, MN987879, MN987651, MN952559; *NVI*, CL. ***V. luzonicum*** Rolfe, *P.W. Sweeney et al. 2321*, YU, MN914772, MN937397, MN987768, MN937428, MN987924, MN987701, MN987835, –, MN987652, –; *Hu 2008*, YU, H. ***V. macrocephalum*** Fortune, *M.J. Donoghue 101*, YU, HQ591604, HQ591673, HQ592027, HQ591745, HQ591911, HQ592153, HQ592086, EF490247, HQ591842, EF462984; *Macgregor s.n.*, A, CL. ***V. microcarpum*** Schlecht. & Cham., *F. Ventura A. 819*, NY, –, –, –, JQ805414, JQ805496, –, JQ805327, KP281898, –, JQ805178; *M.J. Donoghue 32*, YU, H. ***V. molle*** Michx., *M.J. Donoghue & R.C. Winkworth 5*, YU, HQ591606, HQ591675, –, HQ591747, HQ591913, HQ592154, AY627409, AY265185, EF490281, AY265139; *E.J. Palmer 26158*, A, CL. ***V. mongolicum*** Rehder, *M.J. Donoghue s.n.*, YU, HQ591607, HQ591676, HQ592029, HQ591748, HQ591914, HQ592155, HQ592087, EF490248, HQ591844, EF462985; *Teng 1383*, A, CL. ***V. mullaha*** Buch.-Ham. ex D.Don, *M.J. Donoghue WC274*, YU, KF019762, KF019782, KF019838, KF019804, KF019880, KF019903, KF019859, KF019948, KF019927, KF019819; *H. Hara et al. 6302997*, A, CL. ***V. nervosum*** D.Don, *P.W. Sweeney et al. 2298*, YU, MN914773, MN937398, MN987769, MN937429, MN987925, MN987702, MN987836, MN987880, MN987653, MN952560; *A.J.C. Grierson, D.G. Long 2805*, A, CL. ***V. nudum*** L., *E.L. Spriggs 29*, YU, MN914774, MN937399, MN987770, MN937430, MN987926, MN987703, MN987837, MN987881, MN987654, MN952561; *M.L. Fernald et al. 15360*, GH, CL. ***V. obovatum*** Walter, *E.L. Spriggs 264*, YU, MN914758, MN937383, MN987754, MN937414, MN987910, MN987688, MN987822, MN987870, MN987638, MN952548; *R.K. Godfrey, R.M. Tryon 8215*, GH, CL. ***V. obtusatum*** D.N.Gibson, *P.W. Sweeney et al. 3100*, YU, MN914775, MN937400, MN987771, MN937431, MN987927, MN987704, MN987838, –, MN987655, MN952562; *M.J. Donoghue 2359*, YU, H. ***V. odoratissimum*** Ker-Gawl., *R. Olmstead 118*, WTU, HQ591609, HQ591678, –, HQ591750, HQ591916, HQ592157, AY627411, AY265187, HQ591845, AY265141; *W.T. Tsang 25600*, A, CL. ***V. oliganthum*** Batalin, *D.E. Bouffourd et al. 27175*, A, HQ591610, –, –, HQ591751, HQ591917, HQ592158, HQ592088, HQ591804, HQ591846, HQ591971; *E.H. Wilson 805*, A, CL. ***V. opulus*** L., *W.L. Clement 250*, YU, HQ591611, HQ591679, –, HQ591752, HQ591918, HQ592159, –, HQ591805, HQ591847, HQ591972; *L. Holm-Nielsen et al 222*, A, CL. ***V. orientale*** Pall., *Merello et al. 2291*, MO, HQ591612, HQ591680, HQ592031, HQ591753, HQ591919, HQ592160, HQ592089, EF490249, EF490284, EF462986; *R.E. Regel s.n.*, A, CL. ***V. ovatifolium*** Rehder, no molecular data; *E.H. Wilson 240*, A, CL. ***V. pastasanum*** Diels, *P.W. Sweeney et al. 1799*, YU, HQ591634, HQ591694, HQ592050, HQ591774, HQ591941, HQ592181, HQ592103, HQ591814, HQ591858, HQ591982; *Neill 13547*, YU, H. ***V. phlebotrichum*** Siebold & Zucc., *M.J. Donoghue et al. 3*, YU, MN914759, MN937384, MN987755, MN937415, MN987911, MN987689, MN987823, MN987871, MN987639, MN952549; *Mizushima 2930*, A, CL. ***V. pichinchense*** Benth., *P.W. Sweeney et al. 1669*, YU, JQ805257, KP281835, KP281870, JQ805420, JQ805502, KP281886, JQ805332, JQ805580, –, JQ805184; *Croat 98333*, YU, H. ***V. plicatum*** Thunb., *M.J. Donoghue & R.C. Winkworth 10*, YU, HQ591613, HQ591681, HQ592032, HQ591754, HQ591920, HQ592161, AY627412, AY265189, EF490285, AY265143; *Gressitti 1472*, A, CL. ***V. propinquum*** Hemsl., *P.W. Sweeney et al. 2188*, YU, MN914776, MN937401, MN987772, MN937432, MN987928, MN987705, MN987839, MN987882, MN987656, MN952563; *E.H. Wilson 498*, A, CL. ***V. prunifolium*** L., *M.J. Donoghue & R.C. Winkworth 13*, YU, HQ591615, HQ591683, HQ592033, HQ591756, HQ591922, HQ592163, AY627413, AY265190, EF490286, AY265144; *F.D. 1076*, A, CL. ***V. punctatum*** Buch.-Ham. ex D.Don, *P.W. Sweeney et al. 2274*, YU, MN914777, –, MN987773, MN937433, MN987929, MN987706, MN987840, –, MN987657, –; *Feng 63*, A, CL. ***V. rafinesquianum*** Schult., *M.J. Donoghue & R.C. Winkworth 4*, YU, HQ591617, HQ591684, HQ592035, HQ591758, HQ591924, HQ592165, AY627414, AY265191, HQ591849, AY265145; *C.E. Wood Jr. 5599*, GH, H. ***V. recognitum*** Fernald, *Arnold Arboretum 1471-83B/00192902*, A, JQ805261, JX049465, KF019824, JQ805387, JQ805507, JX049490, JQ805337, JQ805585, JX049504, JQ805189; *E. Rouleau 1395*, GH, CL. ***V. rhytidophyllum*** Hemsl. ex Forb. & Hemsl., *M.J. Donoghue & R.C. Winkworth 8*, YU, HQ591618, HQ591685, HQ592036, HQ591759, HQ591925, HQ592166, HQ592092, AY265192, HQ591850, AY265146; *E.H. Wilson*

220, A, CL. ***V. rigidum*** Vent., *W.T. Stearn 1116*, A, HQ591619, HQ591686, HQ592037, HQ591760, HQ591926, –, HQ592093, HQ591807, –, HQ591974; *E. Bourgeau s.n.*, A, CL. ***V. rufidulum*** Raf., *M.J. Donoghue & R.C. Winkworth 14*, YU, HQ591620, HQ591687, HQ592038, HQ591761, HQ591927, HQ592167, AY627415, AY265193, EF490287, AY265147; *S.B. Jones 23635*, PH, H. ***V. sambucinum*** Reinw. ex Blume, *P.W. Sweeney et al. 2100*, YU, KF019751, KF019771, KF019828, KF019793, KF019869, KF019892, KF019848, KF019937, KF019916, KF019811; *B.C. Stone 14420, R. Boeea 10916*, A, CL. ***V. sargentii*** Koehne, *M.J. Donoghue & R.C. Winkworth 17*, YU, HQ591621, HQ591688, HQ592039, HQ591762, HQ591928, HQ592168, AY627416, AY265194, EF490288, AY265148; *B. Bartholomew et al. 1730*, A, CL. ***V. scabrellum*** Chapman, *M.J. Donoghue 82*, YU, JQ805262, KP281836, KP281871, KP281824, JQ805508, KP281887, JQ805338, JQ805586, KP281910, JQ805190; *R.K. Godfrey, R.M. Tryon 54224*, GH, CL. ***V. schensianum*** Maxim., *P.W. Sweeney et al. 2565*, YU, MN914778, MN937402, MN987774, MN937434, MN987930, MN987707, MN987841, MN987883, MN987658, MN952564; *E. Licent 12633*, A, H. ***V. seemenii*** Graebn., *M. Lewis 37409*, GH, JQ805263, –, –, JQ805426, JQ805509, –, JQ805340, JQ805587, –, JQ805193; *A.L. Cabrera et al. 27840*, PH, H. ***V. sempervirens*** K.Koch, *P.W. Sweeney et al. 2191*, YU, MN914779, MN937403, MN987775, MN937435, MN987931, MN987708, MN987842, MN987884, MN987659, MN952565; *Tsang 21630*, A, CL. ***V. setigerum*** Hance, *P.W. Sweeney et al. 2554*, YU, MN914780, MN937404, MN987776, MN937436, MN987932, MN987709, MN987843, MN987885, MN987660, MN952566; *E.H. Wilson 236*, A, CL. ***V. sieboldii*** Miq., *M.J. Donoghue et al. 7*, YU, MN914781, MN937405, MN987777, MN937437, MN987933, MT025844, MN987844, MN987886, MN987661, MN952567; *Walker et al 5658*, A, CL. ***V. stellato-tomentosum*** Hemsl., *M.J. Donoghue 640*, YU, KF019747, –, –, KF019789, KF019865, KF019888, KF019845, –, KF019911, –; *Hemsley 4830*, GH, H. ***V. stenocalyx*** Hemsl., *M.J. Donoghue 60*, YU, HQ591626, –, HQ592043, HQ591767, HQ591933, HQ592173, HQ592097, HQ591810, KF019912, HQ591978; *M.J. Donoghue 60*, YU, H. ***V. suspensum*** Lindl., *M.J. Donoghue & R.C. Winkworth 36*, YU, HQ591629, HQ591692, HQ592045, HQ591769, HQ591936, HQ592176, AY627419, AY265197, HQ591854, AY265151; *E.H. Wilson 1917*, A, CL. ***V. sympodiale*** Graebn., *K.F. Chung 1932*, YU, MN914782, MN937406, MN987778, MN937438, MN987934, MN987710, MN987845, MN987887, MN987662, MN952568; *E.H. Wilson 294*, A, CL. ***V. taitoense*** Hayata, *M.J. Donoghue & K-F. Chung KFC1941*, YU, KF019757, KF019777, KF019833, KF019799, KF019875, KF019898, KF019854, KF019943, KF019922, KF019816; *C.C. Chen 4200*, A, H. ***V. taiwanianum*** Hayata, *W.-H. Hu et al. 2186*, MO, HQ591631, –, HQ592047, HQ591771, HQ591938, HQ592178, HQ592101, EF490253, HQ591855, EF462989; *H. Keng KAO 2550*, A, CL. ***V. tashiroi*** Nakai, *M.J. Donoghue s.n.*, YU, KF019764, KF019784, KF019840, KF019806, KF019882, KF019905, KF019861, KF019950, KF019929, –; *S. Kobyashi 2817*, A, H. ***V. tenguehense*** (W.W.Sm.) P.S.Hsu, no molecular data; *H.T. Tsai 62565*, A, H. ***V. ternatum*** Rehder, no molecular data; *W.P. Fan 3309*, A, CL. ***V. tiliaefolium*** (Oerst.) Hemsl., no molecular data; *M.J. Donoghue 123*, YU, H. ***V. tinoides*** L., *P.W. Sweeney et al. 2167*, YU, KP281816, KP281838, KP281873, KP281826, KP281862, KP281889, KP281852, KP281899, KP281912, KP281843; *P.W. Sweeney et al. 2167*, YU, H. ***V. tinus*** L., *M.J. Donoghue & R.C. Winkworth 35*, YU, HQ591633, HQ591693, HQ592049, HQ591773, HQ591940, HQ592180, AY627420, AY265198, HQ591857, AY265152; *C.H. Godet s.n.*, GH, CL. ***V. trilobum*** Marshall, *Arnold Arboretum 22900A/0174487*, A, HQ591635, HQ591695, HQ592051, HQ591775, HQ591942, HQ592182, HQ592104, HQ591815, EF490290, HQ591983; *W.J. Cody and W.E. Kemp 14872* GH, H. ***V. triphyllum*** Benth., *P.W. Sweeney et al. 1783*, YU, HQ591636, HQ591696, HQ592052, HQ591776, HQ591943, HQ592183, HQ592105, HQ591816, HQ591859, HQ591984; *P.W. Sweeney et al. 1698*, YU, H. ***V. tsangii*** Rehder, no molecular data; *T.T. Yu 18064*, A, CL. ***V. urceolatum*** Siebold & Zucc., *M.J. Donoghue NVI*, HQ591637, HQ591697, HQ592053, HQ591777, HQ591944, –, AY627423, AY265201, HQ591860, AY265155; *NVI*, CL. ***V. utile*** Hemsl., *P.W. Sweeney et al. 2593*, YU, MN914783, MN937407, MN987779, MN937439, MN987935, MN987711, MN987846, MN987888, MN987663, MN952569; *B. Bartholomew et al. 1412*, A, CL. ***V. veitchii*** C.H.Wright, *Bouffourd et al. 27597*, A, HQ591639, HQ591699, HQ592055, HQ591779, HQ591946, –, HQ592106, HQ591817, HQ591861, HQ591985; *B. Bartholomew et al. 374*, A, CL. ***V. vernicosum*** Gibbs, *P.W. Sweeney et al. 2123*, YU, KF019752, KF019772, KF019829, KF019794, KF019870, KF019893, KF019849, KF019938, KF019917, KF019812; *P.W. Sweeney et al. 2122*, YU, P. ***V. villosum*** Sw., *M.J. Donoghue 628*, YU, JQ805280, –, KP281875, JQ805443, JQ805527, KP281892, JQ805357, JQ805600, –, –; *M.J. Donoghue 631*, YU, H. ***V. wrightii*** Miq., *M.J. Donoghue et al. 1*, YU, MN914784, MN937408, MN987780, MN937440, MN987936, MN987712, MN987847, MN987889, MN987664, MN952570; *Muroi 6348*, A, CL.